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ECOLOGY AND BIOENERGETICS OF
THE LONG-BILLED MARSH WREN
Telmatodytes palustris griseus (Brewster)
IN GEORGIA SALT MARSHES

ECOLOGY AND BIOENERGETICS OF THE
LONG-BILLED MARSH WREN IN GEORGIA
SALT MARSHES. 1965.

Page 8, second line from bottom:

"by comparing" should read "and compare"

Page 48, Table 24, under "Assimilation"

"3.8" should read "8.8"

Page 102, Table 50, Percent Ash Weight

97.50 should read 2.50

95.00	"	"	5.00
94.94	"	"	5.06
95.10	"	"	4.90
95.60	"	"	4.40
95.08	"	"	4.92
95.16	"	"	4.84
95.07	"	"	4.93
94.78	"	"	5.22

PUBLICATIONS OF THE NUTTALL ORNITHOLOGICAL CLUB, NO. 5

EDITOR, OSCAR M. ROOT

**ECOLOGY AND BIOENERGETICS OF
THE LONG-BILLED MARSH WREN**
Telmatodytes palustris griseus (Brewster)
IN GEORGIA SALT MARSHES

by

HERBERT W. KALE II

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This paper is based upon a thesis and dissertation submitted in partial fulfillment of the requirements for a M.S. degree and a Ph.D. degree at the University of Georgia (Kale, 1961, 1964). It forms Con-

tribution Number 75 of the University of Georgia Marine Institute, Sapelo Island, Georgia.

Scientific names of North American birds are those found in *Checklist of North American Birds*, American Ornithologists' Union, 1957. I made the line drawings except for Figure 3, which was redrawn from Smalley (1958), and took all the photographs with the exception of Figure 1, which was taken by Eugene P. Odum. The manuscript was submitted to the Nuttall Club 18 September 1964.

HERBERT W. KALE II

Encephalitis Research Center
4001 Tampa Bay Boulevard
Tampa, Florida 33614

ABOUT SAPELO ISLAND . . .

Sapelo Island is one of several large islands, collectively called the "Golden Isles", lying off the coast of Georgia. Sapelo lies approximately six miles from the mainland, about 50 miles south of Savannah and 25 miles north of Brunswick, Georgia. It is accessible only by boat or plane. The island is approximately nine miles long and four miles wide and possesses a diversity of aquatic and terrestrial habitats. There are more than five miles of ocean front with associated sandy and silty beaches and dune developments. Several miles of salt marsh-estuary-tidal creek systems separate the island from the mainland. Sounds and shallow bays lie along the coast to the north and south. Aquatic environments on the island also include several fresh-water ponds, as well as cypress and gum-bay swamps. Terrestrial habitats include old field environments and extensive areas of pine-palmetto and pine-hardwood stands, some of which are essentially virgin in character. Blackbeard Island, a national wildlife refuge, borders Sapelo on the northeast.

Several large Indian kitchen middens, mounds of chiefly oyster, mussel, and conch shells, found on the island provide evidence of human habitation for over 2500 years, and ruins of Spanish and French structures still stand today. In addition to the families of Marine Institute personnel several hundred negroes, the descendents of former slaves who worked in the fields of Sea Island cotton that flourished during the 19th century, now live on the island.

During the past decade Sapelo Island has served as a center for basic research in the natural sciences in the environments of coastal Georgia. This undertaking began with the establishment of the University of Georgia Marine Biology Laboratory in 1953 through the generosity of Mr. R. J. Reynolds (now deceased) and the Sapelo Island Research Foundation. The Laboratory was later reorganized and is presently known as the University of Georgia Marine Institute. Information regarding facilities and research opportunities may be obtained by writing to the Director, University of Georgia Marine Institute, Sapelo Island, Georgia 31327.

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. . . how ample, the marsh
and the sea and the sky!
A league, and a league of marsh-grass, waist-
high, broad in the blade,
Green, and all of a height, and unflecked
with a light or a shade,
Stretch leisurely off, in a pleasant plain
To the terminal blue of the main.

—SIDNEY LANIER
The Marshes of Glynn

INTRODUCTION

In the extensive salt marshes between the sea islands and the coast of Georgia three species of birds are intimately associated with the marsh community, namely, the Long-billed Marsh Wren (*Telmato-dytes palustris*), the Clapper Rail (*Rallus longirostris*), and the Sea-side Sparrow (*Ammospiza maritima*). An analysis of the resident race, Worthington's Long-billed Marsh Wren, *Telmatodytes palustris griseus* (Brewster), in the tidal marshes of Sapelo Island, Georgia, is the subject of this paper. Part I deals with the breeding biology and Part II with the population ecology and bioenergetics.

Sapelo Island, lat 31°20' N and long 81°10' W is in McIntosh County and is approximately 50 miles south of Savannah, Ga.

Few studies of the population structure of salt marsh birds appear in the literature. Studies on the breeding biology of the Long-billed Marsh Wren have been made in fresh water marshes by Welter (1935) at Ithaca, N.Y., and Verner (1963a, 1965) in the state of Washington; and by Wheeler (1931) in coastal marshes of Alabama. Johnston (1956) has intensively studied the Song Sparrow (*Melospiza melodia samuelis*) in California salt marshes.

A host of laboratory studies on bioenergetics of birds are in the literature, including: Benedict, 1938; Koch and de Bont, 1944; Brody, 1945; Kendeigh, 1939, 1941, 1944, 1949, 1963; Seibert, 1949; Pearson, 1950, 1954; Salt, 1953; Wallgren, 1954; Davis, 1955; Rautenberg, 1957; West, 1960; Cox, 1961; King, 1961; Graber, 1962; Kahl, 1962, 1964; Lasiewski, 1962, 1963; Helms, 1963. Activity patterns and time budgets in several species have recently received increased quantitative study (Lees, 1947; Kluiyer, 1950; Gibb, 1954, 1956, 1960; Gibb and Betts, 1963; and Verner, 1963a).

Few attempts have been made to estimate the total energy flow through an avian population in its natural ecological system. Pearson's (1954) work with the daily energy requirements of a wild Anna Hummingbird (*Calypte anna*) is perhaps the first to point in this direction. Connell (1959) studied the population energy flow in Savannah Sparrows (*Passerculus sandwichensis*) wintering in old fields of South Carolina (see Odum, Connell, and Davenport, 1962). Kahl (1964) has presented some estimates of energy flow in the Wood Stork (*Mycteria americana*) populations of south central Florida. Uramoto (1961) has made preliminary estimates of respiratory energy and food consumption in populations of adult birds in a broad-leaved

deciduous forest of central Japan. More recently Brenner (1963) studied the energy flow in two breeding populations of Red-winged Blackbirds (*Agelaius phoeniceus*) in fresh water marshes of Pennsylvania.

As this paper was being prepared for publication the results of LeFebvre's (1964) research on the use of D_2O^{18} for measuring energy metabolism in the pigeon (*Columba livia*) at rest and in flight were published. This new method for determining energy requirements of wild species in their natural environment holds much promise.

THE GEORGIA SALT MARSHES

The Georgia salt marshes, in a network of tidal rivers and creeks, form a belt about eight kilometers wide between the sea islands and the mainland. Over most of this vast area the marshes support pure stands of marsh or cord grass (*Spartina alterniflora* Loisel). (Fig. 1). Detailed descriptions of this marsh system were made by Galtsoff and Luce (1930), Oney (1954), Ragotzkie and Bryson (1955), Smalley (1958), Teal (1958), and Kuenzler (1959). Smalley (op. cit.) divides the *Spartina* marshes into four major types as shown in Fig. 2: (1) streamside marsh with tall grass two meters or more high (Fig. 1, 5, 6) (2) levee marsh with grass of moderate (1-1.5 meters) height (3) high marsh with grass seldom exceeding one meter and (4) middle marsh, with *Spartina* taller than the grass in the high marsh, but sparser and at a lower altitude. This fourth type occurs primarily where there is extensive anastomosing of small creeks or drainages. Figure 3 (from Smalley, op. cit.) illustrates the distribution of marsh types 1, 2, and 3.

During the breeding season *T. p. griseus* is restricted primarily to streamside and levee marshes, but may be found in some areas of middle marsh where there are stands of *Spartina* over a meter in height. During the winter when individuals of more northern races join the resident race the wrens forage more widely over the *Spartina* marsh and are occasionally observed in stands of Black Rush (*Juncus roemerianus*), which grow at higher elevations.

STUDY AREAS

I did the major portion of my field work from 1958 through 1961. Wren censuses were made from 1959 through 1962, and laboratory studies during 1962 and 1963. Studies on bioenergetics of captive birds were carried out at the biological laboratories of the University of Georgia at Athens.

I made observations in three study areas in 1958 and two in 1959-1961 in the salt marshes of the Duplin River watershed. The eastern limit of the watershed is marked by Sapelo Island, and the western limit is indicated by the dashed line (from Pomeroy, 1959) in Fig. 4. The marshes are near the laboratory of the University of Georgia Marine Institute. The area comprises approximately 1047.9 hectares, or 2600 acres, including 165.9 hectares (410 acres) of the Duplin River surface area at mean low water (Ragotzkie and Bryson, 1955).

Study Area 1 in 1958 extended for approximately 0.33 kilometers along the east bank of the Duplin River (Fig. 6), an elongated tidal bay of Doboy Sound, and contained approximately twelve territories. It consisted of narrow strips of tall marsh grass interspersed with stretches, varying in size, of shorter grass, the latter the result of erosion and slumping of the levees.

Area 2 was located along the north bank of Barn Creek (Fig. 5), a tributary and distributary of the Duplin River. It was about 0.32 km in length. This area was characterized by a continuous broad strip of tall streamside and levee *Spartina*. In 1959-1961 this area was expanded to include several more territories, making a total length of 0.40 km.

Area 3, along both banks of Barn Creek, contained essentially streamside and levee marsh. It was about 0.38 km long. The area was abandoned by the wrens shortly after mid-May in 1958 and was occupied by only three singing males in 1959. Therefore it has not been included in the remainder of this study.

In 1959-1961 Area 4, along the east bank of the Duplin River, extended from the mouth of Barn Creek to a point opposite the north end of Little Sapelo Island, a distance of approximately 0.74 kilometers. This area was similar in habitat to Area 1. It differed in that it contained several territories that were in a continuous band of *Spartina*.

PROCEDURES

During the breeding season I generally visited the study areas at least once each week, sometimes more often. Occasionally ten days elapsed between visits. In 1960 weekly visits were not begun until 1 June. Prior to that date approximately three weeks elapsed between each visit.

I determined the location of territories and nests by observing the movements of singing males. Narrow cane poles, approximately equal in diameter to *Spartina* stems, with the top foot or so painted a bright color to facilitate observation, were placed near each female nest. In Area 2, where the grass was more dense and extensive, poles were also placed near each male nest or group of male nests. Small green cardboard tags on which was recorded the first date of observation were tied to one of the supporting stems of each nest.

Nest data and other observations were transcribed from a field notebook to an index card kept for each territory.

When possible I banded young wrens just prior to fledging with United States Fish and Wildlife Service aluminum bands. In 1959 and 1960 I also used colored plastic bands.

In June of each year 1959-1962 censuses of singing territorial males were made over a one to two week period. Singing males could be counted easily as I moved slowly along the network of tidal creeks in a small boat at high tide. I recorded the location of each male or cluster of recently built nests on an aerial photograph. By censusing at high tide I could reach all wren territories at a time when each wren was forced to occupy the upper portion of the marsh grass. Almost 900 hectares (over 2000 acres) were covered in this manner annually. Calculation of total density was based on ratios of breeding to non-breeding males and males to females as determined by observations in the study areas.

The area of the Duplin River watershed was computed by using a planimeter and a United States Coast and Geodetic Survey Chart of Sapelo and Doboy Sounds (CG & S Chart 574).

From direct observations and aerial photographs I estimated available habitat to be between 8.1 and 12.1 hectares or an average of 10.9 hectares (25 acres) of inhabitable marsh, upon which is based the specific or ecological density. The area actually utilized by wrens was found by multiplying the total number of pairs of wrens observed by the mean territory size maintained by a male.

I followed the concepts and terminology of Odum (1959) in estimating natality and mortality of the populations. Realized or ecological natality is defined in this paper as the average number of young hatched per pair of adults.

For the first brood fledgling survival through the first week was estimated by observing how soon after fledging the adults began a second brood. The adults continue to feed and care for the young for a period of at least two weeks before beginning a second brood. Starting of a second nest within four or five days after fledging of the first brood was a good indication that the fledglings did not survive.

I determined losses from drowning by high spring tides in two ways: First, by being present in the marsh during high water and observing those nests that were submerged. Second, by observing nests the day after a high spring tide. Nests that have been immersed remain wet, and often the interior of the nest and the eggs—if the eggs have not been carried away by the water—are covered with a fine layer of mud for several days.

Desertion was determined when a new nest with eggs appeared very near an earlier nest with eggs that were no longer being brooded. Desertion figures do not include those nests covered by high tides that were subsequently abandoned.

All specimens collected were analyzed either shortly after collection or after storage in plastic bags in deep freeze. After determination of weight, age and sex, wing length measurements (chord measurement) were taken and the stomach contents preserved for study. Total dry weight was determined after drying to constant weight in a vacuum oven at 40°C or, in a few cases, in an ordinary drying oven at 100°C. Most specimens were put through a fat extraction process as described by Odum (1960) but modified as follows: Instead of grinding the frozen carcass in a chilled meat chopper, I opened the bird for determination of age and sex. The breast muscles were then cut into several sections, and the carcass was placed in a vacuum oven at approximately 40°C until dry. The bird was then ground in a Waring blender with 95% ethanol, poured into a breaker with petroleum ether and placed on a steam bath. When the solution began bubbling freely it was poured onto a fine mesh screen, the filtrate squeezed out, and the residue replaced in a beaker with petroleum ether and again brought to boil on the steam bath. This procedure was repeated until the filtrate was clear. Two or three ether washings were sufficient to extract all of the lipids. Dry residues were then ashed in a muffle furnace at 500°C.

A few adults and immatures collected at various seasons were kept for determinations of total caloric content in a Parr Adiabatic Bomb Calorimeter. I tried two approaches: (1) Samples of ground tissue of whole specimens were burned in the calorimeter, and (2) non-fat

dry residue and the extracted fat were bombed separately. All caloric values are expressed in terms of ash-free dry weight. Because some ash is lost in the bomb calorimeter where the heat of combustion in pure oxygen is high, a correction factor based on wrens ashed in the muffle furnace was applied. For whole marsh wrens 5.8% of ash was estimated to be lost in the calorimeter.

Stomach contents of all wrens collected were examined. The number of species of salt marsh insects and spiders, the chief food of *griseus*, is low, with strong dominance by a few species. Thus it was possible to identify species in many cases. Volumetric measurements were made of stomach contents, and dry weights of some food items were also determined.

I tried two methods of sampling the insect and spider populations in the marsh, namely, (1) the removal sweep method as described by Menhinick (1963) and (2) the bag technique in which a large cloth bag was dropped over a square meter of grass and then removed to the laboratory for recovery of trapped arthropods. The height of the grass and softness of the mud substratum precluded using the sweep method in the streamside marsh. Sampling of the medium height grass on the levees, in which the wrens feed, was possible, but only a few samples were obtained in occupied wren territories.

The caloric value of the insects and spiders that are eaten by wrens was determined by combustion in the bomb calorimeter for each species when sufficient numbers were available; otherwise for lumped groups of species.

Daily energy requirements were determined for hand reared adult wrens obtained from nests in 1961 and 1962 at age seven to twelve days. The young wrens easily became adapted to captivity and were in little danger of injuring themselves. The nestlings were fed hourly or more often on live mealworms (larvae of *Tenebrio molitor*), small grasshoppers, collected by hand or sweep net, and a moist mixture of liver, fish, ground beef (1:1:1), pulverized Growena game bird food, and Pabulum. Young birds were permitted to fly about the room but they were usually content to remain in clusters of *Spartina*. As soon as they reached the independent stage they generally reverted to a relatively wild state and became aggressive toward one another during the day (but roosted together at night) so that it was necessary to keep them caged separately.

Adults were maintained on a daily diet of live mealworms and the previously described mixture. Captives maintained weights similar to those of collected wild wrens, although by the end of the experiments they contained more fat than did wild wrens. Fat free weights of these wrens were similar to those of wild wrens. Molt and song cycles resembled those of wild birds.

I determined energy requirements of ten wrens (seven males and

three females) over a two year period by two different methods of indirect calorimetry: (1) Measurement of food consumption by the method described by Kendeigh (1949), and (2) measurement of oxygen consumption.

To study energy intake, birds were weighed and confined individually to Hendryx cages ($22 \times 32 \times 35$ cm), the floor of which was lined with aluminum foil of known weight. A quantity of mealworms was weighed to the nearest hundredth of a gram on an Ohaus triple-beam balance and placed in a feeding cup each day. The wren mixture was daily rolled into "worms," weighed, and placed in another container. Several grains of Hartz Mountain bird gravel were supplied weekly. In the salt marsh natural grit is obtained in the form of tiny molluscs (*Littorina irrorata*, *Melampus bidentatus*, and *Littoridinops* sp.), and the tough chitinous parts of spiders and insects, e.g., chelae, jaws, legs, and heads. At weekly intervals the birds were weighed and the cages cleaned and all excreta and uneaten food separated by hand picking. The excreta and the uneaten wren mixture were dried to constant weight. The uneaten mealworms were weighed while still alive. Wet, dry, and ash weights of mealworms and wren mixture were determined, as well as the caloric value of all food and excreta.

The food consumed by each wren was multiplied by its energy content to obtain the gross energy intake of the bird for the period. Caloric values determined for each batch of wren mixture were used in the calculations of data for birds fed the batch. Energy loss in the excreta was found by multiplying its energy content by the dry weight of the excreta for the period. The excretory energy was then subtracted from the gross energy intake to yield the available metabolic energy, or assimilated energy. Any loss or gain in weight in excess of 0.25 g was multiplied by 7.0 Kcal and added to or subtracted from the available metabolic energy. The resulting value is the respiratory or existence energy.

Weight loss was assumed to represent, in part, fat catabolism, and weight gain, in part, fat anabolism or storage. A value of 7.0 Kcal/g, instead of 9.0 Kcal/g, the caloric equivalent of the wren fat, was used here because *griseus*, being non-migratory, is not known to accumulate large amounts of fat. During the breeding season weight changes are the result of changes in gonad size as well as changes in fat metabolism. The choice of a caloric value halfway between fat and protein is perhaps arbitrary. But this choice does not alter significantly the results obtained since weight gains or losses were relatively small.

Since the consumption of oxygen by animals is often used to determine energy requirements, I decided to measure oxygen consumption by comparing the metabolic rates obtained in an oxygen respirometer with rates obtained by the feeding experiments. Oxygen consumption

was measured in an apparatus described by MacLagen and Sheahan (1950), as modified by Wiegert (1961). Unlike Wiegert's design, however, a smaller Pyrex desiccator (220 mm diameter) was used and the kymograph was omitted since wrens were not kept in the chamber for longer than a three hour period. In addition, to avoid the effect of external atmospheric pressure changes, a five gallon carboy was hooked to the arm of the manometer, which normally is open to the external atmosphere. With the use of glass "Y" connectors and additional three-way stopcocks, several chambers were set up simultaneously.

I determined oxygen consumption at various temperatures, chiefly between 22°C and 35°C. Readings below room temperature were obtained by placing the desiccator in a tub of water and adding ice, while higher temperatures were obtained by inserting a heating element, with thermostat, in the water.

For some of the determinations an effort was made to approach basal conditions as nearly as possible, but the restless behavior of the wrens when restrained inside a small darkened box, and the fact that most of the measurements were made during the day, did not give results indicative of wholly basal conditions. Nevertheless, sufficient data were obtained to make an estimate of basal metabolism and to permit comparison with the feeding experiments.

Carbon dioxide production was measured on 25 May 1963 with a Beckman L/B Infrared CO₂ Analyzer (Model 15A) at the Laboratory of Radiation Ecology, Savannah River Plant, Aiken, S.C. Respiratory quotients (RQ) for active and inactive wrens and a mean oxycaloric coefficient were calculated. Because the diet fed to the experimental birds remained the same regardless of season, this coefficient was assumed to be similar for all wrens throughout the study.

On the basis of the field data collected throughout the breeding seasons of 1958-1961, total standing crop at weekly intervals in grams ash-free dry weight and kilocalories per square meter of occupied habitat were calculated for the study areas. Production and respiration for each interval were also calculated and total energy flow for each season estimated.

Part I
BREEDING BIOLOGY
RESULTS

START OF BREEDING

General. Male Long-billed Marsh Wrens begin singing on their territories in early March at Sapelo Island. At first, singing is sporadic and territories are not actively defended. During periods of warm weather singing is intensified, and several males may be heard singing in an area that later on will become the territory of a single male. Occasionally these extra males are members of a northern race. By mid-April most of the territories are occupied by singing males. In 1958 and 1960 the first male nests—those nests built by the male and generally not used by the female—appeared by mid-April. The first egg in 1958 was found on 23 April, and by 27 April the first clutch was completed. In 1959 the first completed male nest was found on 29 March, and the first egg was observed on 8 April. This clutch was completed by 15 April. In both 1958 and 1959 the period between the finding of the first male nest and the first egg was not more than eight to ten days. In addition, once nesting began, the majority of the early clutches were completed during the same period of time. In 1960 and 1961 the precise period between appearance of the first male nest and the first egg was not determined. However, in 1960 eggs were not found in nests until late April, while in 1961 eggs appeared early in April.

The seasonal incidence of nesting in 1958 and 1959 is shown by Fig. 7. In 1958, 24% of all the completed clutches were laid during the period 26 April-3 May. In 1959, 16% of all the completed clutches were laid during the period 12-19 April. In both years the first peak represents first nesting attempts and is higher than any subsequent peak. In 1958 three major nesting peaks occurred. The first peak was followed by a second major peak after a six week interval. Based upon observations of 16 pairs of wrens, six weeks is the minimum length of time between start of a first brood and start of a second brood. Verner (1963a) has noted a similar interval between laying peaks of marsh wrens in Washington. The second peak represents some second brood attempts, several first nesting attempts, and several renestings. A renesting is a nesting attempt made following a nesting failure. The third major peak includes second brood attempts and renestings.

In 1959 a second major peak appeared six weeks after the first peak just as in 1958. By this time, however, predation had increased to such an extent that no further major nesting peaks were observed. Instead, a series of smaller peaks represent renestings and second brood attempts. A single third brood attempt is reflected here also. Increased pressure of predation completely obscured first and second brood cycles in 1960-1961, hence graphs showing occurrence of nesting in these years have not been presented.

Pair formation. The presence of males and females in the marsh throughout the winter months and the secretive habits of both sexes at this time precluded the determination of the precise time of pair formation. Several females were seen in established male territories in late March and early April. This indicates that pair formation was occurring at the time. Though copulation was not observed, courtship displays and chasing were noted on numerous occasions.

Polygamy. I rarely observed a polygamous male. In 1958 two instances of bigamy were noted. In one male territory two female nests were approximately five meters apart. Both nests were robbed shortly after incubation began. In another territory two females made the second brood attempt. Two nests about four meters apart were found with eggs on the same day, along with the two females. Several days later one of the nests was robbed and only one female remained in the territory.

In 1959 there was one case of suspected bigamy. During the third unsuccessful nesting attempt two female nests with eggs were found. Both of these were robbed shortly thereafter and no more nesting attempts followed.

In June, 1960, I observed two polygamous males. In both instances the nests were robbed and only a single female remained in each territory. In late May, 1961, one bigamous male was noted. Again, both nests were robbed and only one female remained to attempt further nesting.

Over the four year period, then, only six instances of polygamy, or possible polygamy, were observed. This represents only 5% of all the males studied. None of these males remained polygynous through a complete brood cycle.

Unmated or bachelor males. During this study I noticed that no female nests were built in five of the actively maintained territories. Neither were any females observed. In each case the quality of the habitat was inferior to that of surrounding territories. In one instance the territory size was relatively small (28 m²). In another the tall grass was very sparse. In the others the grass height was barely over one meter throughout the territory. Of 126 males studied, five, or approximately 4% were unmated. This percentage may actually be somewhat higher for the population in the watershed because the

majority of the territories in the study areas were located in good wren habitat.

TERRITORIALISM AND SONG

T. p. griseus delimits his territory by singing at one end of it for several minutes and then moving to the other end and singing there. This movement may be in a direct flight over the top of the grass or it may be accomplished by fluttering to a height of 3-5 meters, then dropping down into the opposite end of the territory. The whole of this aerial display is accompanied by a song, the last phrase of which is completed in the grass.

The male sings everywhere in the territory—down in the dense grass or near the tops of tall dead flower stalks remaining from the previous year's crop of *Spartina*. Singing reaches a peak in late April or early May and remains at a high rate from May to July. The average number of songs per minute without interruption is approximately ten with a maximum of thirteen. Countersinging frequently occurs with males of nearby territories.

Frequently, between periods of regular singing, males make their presence known by a steady humming song resembling the sound of a motor idling out of gear. This song is often heard between repetitions of the full song.

Occasionally a wren will sing at night, especially at the time of the full moon. However, there are no periods of sustained singing. Instead, singing is only intermittent throughout the marsh.

By mid-August only an occasional adult song is heard in the marsh. About this time immature males from the earliest nestings begin to sing. This subsong possesses the basic pattern of the breeding adult song, but it is shorter in duration, does not have as many notes, and is very weak in volume.

Defense of the territory manifests itself primarily in song. But when opponents meet face to face, display becomes the important defensive or offensive mechanism. This consists mainly of fluffing out the body feathers, holding the tail erect to the extent that it almost touches the back of the head, bobbing or swaying from side to side, and humming or singing. I observed no instances of actual fighting, i.e., body contact.

T. p. griseus generally tolerates other species of birds. The female sometimes is upset when Boat-tailed Grackles (*Cassidix mexicanus*) are in the territory. On the other hand, in 1959 grackles and wrens nested side by side in the tall *Spartina* in several of the Barn Creek territories. In early May I watched a male wren fly at a Seaside Sparrow, which had just flown into the territory. This same male ignored a migratory Sharp-tailed Sparrow (*Ammodramus caudacuta*),

which was singing nearby. Most of the time, however, the wrens do not pay any attention to the marsh emberizids. The Seaside Sparrow, for instance, feeds primarily on the ground, whereas the wrens feed on the small arthropods and molluscs living on the *Spartina*. I have never collected a marsh wren with muddy feet, or a Seaside Sparrow with clean feet.

Most territories are maintained throughout the breeding season, as long as a pair of wrens is raising a brood. As the season progresses the presence of fledglings and the adults feeding them, and immatures now on their own, is tolerated by males on territory. Apparently during this time, as long as individuals make no attempt to challenge the males' proprietary rights, their presence in the territory is allowed.

Unless there is a third brood attempt, of which only one was observed over the four-year period, active defense of the territory ceases after the second brood is fledged. Often the territory is abandoned completely. Desertion of a territory may also occur after repeated nesting attempts have all ended in failure. Whether the adults in my study areas actually deserted or were killed was not known in most cases. If desertion occurred early in the season, I assumed that the birds moved elsewhere and established breeding territories. Abandonment later in the season after unsuccessful nesting attempts probably resulted from slowing of breeding activities. Almost all breeding activities are completed by the end of August.

Welter (1935) found that new territories for second broods in cattail and sedge marshes were established in more open areas than those used for the first brood. The tall dense growth of cattail (*Typha angustifolia*) probably necessitates this. The taller summer growth of *S. alterniflora* actually improves, or adds to, many territories of salt marsh wrens. The *Spartina* growing on the streamside marsh is quite tall by July and is a meter or so above the high tide level, thus making more grass available to the wrens. Increased height offsets the loss of feeding surface that occurs in the lower part of the stem as the plant grows. By July the lower portion of the stem is devoid of leaves, and thus does not harbor as many insects and spiders. I found no evidence of a male moving to an entirely new territory to raise a second brood. Only slight modifications in boundaries occurred. Verner (1963a) noted some seasonal shifting of boundaries by marsh wrens in Seattle marshes, but almost none in marshes of eastern Washington.

NIDIFICATION

Early male nests are located from one half to one meter above the surface of the mud. As the grass grows taller, subsequent nests are constructed higher. By the end of the breeding season some nests

are as much as two meters above the marsh bed. Most nests, however, are approximately 1.0-1.5 m above the sediments.

Nest construction by other races of marsh wrens, *T. p. dissaëptus*, *T. p. marianae*, and *T. p. palustris*, has been thoroughly described by Welter (1935), Wheeler (1931), and Miller (1906) respectively. The nests of *T. p. griseus* are similar in size and appearance to those of these races, but differ in that the major construction material is *Spartina* (see Figs. 8 and 9). Verner (1965) determined the total number of grass strips and cattail down in three nests of marsh wrens in Washington and estimated that an average nest contained 100 pieces of down and 476 strips, and required 9.3 hours for construction.

Male nests in every stage of construction are found. Some are well built, while others are just loose balls of grass. The primary characteristics of a male nest are (1) an entrance hole of larger diameter than that in a female nest and (2) an unlined interior. The number of male nests found in a territory varied widely. From 3 to 27 per territory per year were built during the present study. The mean number of male nests per territory throughout the season was 12.3 in 1958, 11.9 in 1959, 6.1 in 1960, and 10.1 in 1961.

Verner (1965) reported an average of 20 male nests per territory. He included only males that were present in territories for the entire breeding season. My data includes all males observed, whether present during the entire season or not. Omitting these males increases the mean number of nests per territory only to 13.1, 15.3, 6.6, and 10.6 for each of these years 1958-1961 respectively. Welter (1935) found that "five nests is a fairly good average for a single male bird" while several built as many as 10 nests. Since most male nests built during April and early May have disappeared by mid-June, the male is continually building new nests.

Occasionally *griseus* uses male nests as dormitories. Several times I observed an abundance of fresh feces on the outer edge of the nest opening, indicating that a bird had spent the night in the nest. Skutch (1940) concluded that of 14 species of wrens, 11 sleep in nests constructed by themselves.

The female, or breeding, nest is lined with shreds of dead *Spartina* leaves, feathers of the Clapper Rail, egrets, and wrens, and occasionally raccoon and Rice Rat hairs. A projecting sill just inside the entrance forms a "tunnel" into the interior of the nest. An active nest with eggs frequently has a soft plug of finely shredded *Spartina*, feathers, and mammal hair. This plug may be part of the sill, or it may be used to fill the entrance. Completion of the female nest takes about five days. Verner (1965) found that usually three days were required for completion of male nests by marsh wrens in Washington.

Welter (1935) at Ithaca reported that females usually built the breeding nest. But Verner (1965) in Washington observed only five

females participating in nest construction prior to lining them, and concluded that females usually accept one of the male courting nests, especially for renesting purposes. If the female started a new nest, the male contributed the major share of construction.

My impression is that *griseus* females generally did not use the male courting nests. Breeding nests were usually less than a week old when the first eggs were laid. This fact suggests that construction was started for breeding purposes only. I made no attempt to determine which sex built the outer shell of the breeding nest. However, on eight different occasions, three times in 1958 and five times in 1959, after failure of earlier nesting attempts, females completed male nests and laid eggs in them.

If the first nesting endeavor of a female meets with disaster, a renesting attempt is usually made, though not always. If it is early in the season, the new effort begins immediately. Some females appear to be more persistent in their desire to nest than do others. Some wrens after a nesting failure do not make a second attempt. Some make repeated endeavors until a nest is successful. During this study two females each made six nesting attempts before being successful. Three others renested five times each, but only one nest successfully fledged young.

Second brood nestings are begun from one week to a month after fledging of the previous brood. Only 26, or approximately 17%, of 154 nesting attempts over the two year period 1958-1959 represent second brood attempts. In 1958, 12 out of 46, or approximately 27% of the nesting attempts, were second brood nests. In 1959, 14 out of 108, or approximately 13% of the attempts, were second brood nests. I observed no second brood efforts in 1960 or 1961.

In 1959 a third brood attempt was unsuccessful when the nest was robbed after three eggs were laid.

Wren nests, especially old or unused nests, are used by several other marsh inhabitants. A common occupant of nests once they have become damp from tides or rains is the small (2-3 cm) Square-backed Crab (*Sesarma cinereum*). Several times I have encountered Vespid wasps that constructed their paper nests inside male nests. One of the most common inhabitants of wren nests in 1959-1962 was the Rice Rat (*Oryzomys palustris*). This rodent is essentially nocturnal and prefers to remain hidden during the day. The dark protective interior of a wren nest provides a convenient dormitory or brood chamber for the rat.

EGG LAYING AND INCUBATION

Egg laying begins soon after completion of the female nest. Usually one egg is laid each day until there is a clutch of three to five eggs.

On two different occasions females laid two eggs on consecutive days, then delayed laying for several days before completing the clutch. Table 1 shows the number of nests containing completed clutches and

TABLE 1
FREQUENCY OF 3, 4, AND 5 EGG CLUTCHES IN NESTS OF *T.p. griseus*,
SAPELO ISLAND, GEORGIA, 1958-1961

No. of Nests	No. of Eggs per Completed Clutch	Percent Frequency of Completed Clutches
113	5	58.85
62	4	32.30
17	3	8.85
192		

the frequency of 3, 4, and 5 egg clutches. Five is the most frequent number, while very few clutches contain only three eggs.

Table 2 shows the variation in clutch size throughout the breeding season. The season has been arbitrarily separated into three periods of approximately six weeks each. Six weeks, as mentioned previously, represents a complete brood cycle, but since overlapping occurs, the division of the season into three periods remains somewhat arbitrary. There is only a slightly significant difference between the first and second periods ($.10 > P > .05$). There appears to be a significant difference between the first two periods and the last ($P < .01$). The last period represents a large number of renesting clutches, which tend to be smaller than in earlier attempts. Verner (1965) also found that clutch sizes at the end of the season were smaller than at the beginning.

Figure 10 presents graphically a breakdown of frequency of clutch size. Most nests during April-June contain five eggs, whereas the last period is characterized by a smaller clutch size.

Egg laying takes place early in the morning. My observations indicate only that this occurs prior to 8:00 AM. Welter (1935) also reports early morning laying.

Incubation periods range from 12 to 14 days counting from the date of the last egg laid to the date of the last egg hatched. Table 3 presents the incubation periods for 35 nests in 1958 and 1959. The average incubation period is 13 days. This agrees with the findings of Welter (1935). Verner (1965), however, found incubation periods ranging from a little over 13 days in July to over 16 days in April.

Hatching of all the eggs occurs within a 24-48 hour period. Some eggs may begin hatching 11 days after the last egg is laid. This indicates that incubation begins one or two days prior to laying of the last egg. Verner (1965) has found this to be true by direct observation of numbered eggs.

TABLE 2							
VARIATION IN CLUTCH SIZE, 1958-1961							
Year	12 Apr.-24 May Number of Nests	Mean Clutch Size	25 May-5 July Number of Nests	Mean Clutch Size	6 Jul.-10 Aug. Number of Nests	Mean Clutch Size	Annual Mean $\pm$ S.E. S.D.
1958	14	4.86	10	4.60	8	4.00	4.56 $\pm$ 0.11 0.62
1959	43	4.67	28	4.82	4	3.75	4.68 $\pm$ 0.07 0.57
1960	4	4.50	18	4.50	15	3.66	4.16 $\pm$ 0.12 0.73
1961	23	4.74	22	4.18	3	4.00	4.44 $\pm$ 0.09 0.65
1958-61	84	4.71 $\pm$ 0.06	78	4.54 $\pm$ 0.07	30	3.80 $\pm$ 0.11	
S.D.		0.50		0.64		0.61	

TABLE 3
LENGTH OF INCUBATION PERIOD, 1958-1959

Number of Nests	Incubation Period* (Days)
8	12
15	13
12	14
35 Nests	Range: 12-14 days Mean: 13.1 days

* Number of days from date last egg was laid to date last egg was hatched.

In 1958 four eggs of known age were artificially incubated for the last eight days of incubation. Each of these eggs hatched on the thirteenth day of incubation.

Whether the male assists the female in incubating the eggs is doubtful. Welter (1935) concluded that he does not. Miller (1906) stated that he observed both parents incubating the eggs in Pennsylvania. Verner (1965) reports that incubation is performed solely by the female and that only the female develops a brood patch. During the breeding season the male must maintain his territorial boundaries. When a male disappears, the males on either side of his territory are quick to notice this, and they immediately extend their boundaries. A male brooding eggs implies an undefended territory. An example of the importance of continual vigilance on the part of the male, in maintaining his territory was noted in one of my collecting areas. Two singing males from adjacent territories were shot within a five minute period. Within the next 15 minutes the male from a third territory moved into the territories of the two collected males.

During the peak of the breeding season, May-July, I did not hear any male remain silent for any length of time when other males were singing nearby. Furthermore, males rarely showed any concern, other than curiosity, when I was near a nest where incubation was in progress, but the female became greatly agitated. This lack of concern by the male when a human intruder is near the nest was also noted by both Welter (1935) and Wheeler (1931).

CARE OF THE YOUNG

Soon after the eggs hatch the shell fragments are removed and both parents begin feeding the young. The female undertakes most of the care of the nestlings. Verner (1965) did not observe males carrying food to nestlings until the oldest young was about two days old. He found both parents regularly feeding young in one wren population in Washington while in another population males did not

feed young during the first brood but did during the second. Welter (1935) stated that "no male has been observed bringing food to the young." Miller (1906) and Shufeldt (1926-27) are of the opinion that both adults care for the nestlings.

Only twice did I observe males feeding nestlings. It was not determined whether or not the male in every territory assisted in the care of the young. The lack of concern shown by many males, where there was a nest of young, indicates that the male plays a subordinate role, if any, in the care of young. His first duty is the maintenance of territorial integrity.

The length of the nestling period is about 12 or 13 days. If left undisturbed the young may remain in the nest 13-15 days; if disturbed, young birds will flush after the tenth or eleventh day, even before they can fly. Figs. 9 and 11 show a captive 11-day-old wren.

Since the male usually does not abandon his territory after the first brood, his assistance in feeding the fledglings is probably limited to his territory. During the first week fledglings generally remain in the vicinity of the nest. Movement is in either direction along the levee, but not more than one or two territories away. As the young become more independent, they move further away from the nest territory and congregate with other immature wrens. One wren, banded as a nestling on 11 May, was found over 0.6 km from the nest on 17 June, in company with several other immature wrens.

DISCUSSION

START OF BREEDING

Figs. 12 and 13 indicate that nesting began when the daily mean temperatures were above 15°C. This correlation is more apparent in 1958 and 1959. The period of first nesting in 1959, though two weeks earlier than in 1958, occurred during a similar temperature regime. In 1960 and 1961 the exact dates of appearance of the first male nest and of the first egg were not determined; however, these dates fall within the 2-3 week period indicated in Fig. 13 (a male nest was observed in one territory during a warm spell in early March, 1961). The spring of 1961 was very mild beginning in early March, whereas temperatures below freezing occurred in March, 1960. Nice (1937) found that the start of laying by Song Sparrows (*Melodia melospiza*) is closely correlated with temperature. Johnston (1956), on the other hand, was unable to show correlation between nesting of salt marsh Song Sparrows and the temperature of their environment. Verner (1963a) could not draw any definite conclusions about temperature and the start of nesting by marsh wrens in Washington, but felt that initiation of breeding activity was influenced by the suitability of the habitat and by weather conditions (Verner, 1965).

The low incidence of polygamy reported in this study is at variance with observations by Welter (1935) and Verner (1964, 1965). Welter concluded from his study that the male wren is essentially polygamous. He found between one fourth and one third of the territories were inhabited by two females and one male. Verner found over 30% of the males were polygamous in western Washington marshes and 50% of them polygamous in eastern Washington. Kendeigh (1941) reported that 6% of House Wren (*Troglodytes aedon*) matings are polygamous. Armstrong (1953) found that 50% of European Wrens (*Troglodytes t. troglodytes*) are polygamous, but that the St. Kilda Wren (*T. t. hirtensis*) is monogamous.

In a discussion of polygamy among birds, particularly wrens, Armstrong (1955) associates the existence of polygamy with an adequate food supply. Where food is fully available, the services of the male are not required in raising the young. This leaves the male with considerable "time on his hands" and thus enables him to become polygamous. Conversely, in harsher habitats where it is necessary for both parents to share in feeding the young the male does not have time to become polygamous. Earlier Armstrong (1953) had suggested "thus it appears that the wrens in bleak insular habitats tend to be monogamous, while those of southern continental habitats incline to polygamy."

The foregoing summarization of Armstrong's hypothesis may apply to races of *Troglodytes troglodytes*, but certainly not to the races of *Telmatodytes palustris*, where in three of the northern races, *dissaëptus* (Welter, 1935) *paludicola*, and *plesius* (Verner, 1964), 25 to 50 percent of the males are polygamous, and in one of the southern races, *griseus* (Kale, present study), only 5% are polygamous.

One of the most obvious differences between the northern populations and the Sapelo population is in the size of territories (see comparisons in later discussion of territoriality and social behavior). In the northern fresh water marshes territories are considerably larger than on Sapelo Island. The northern wren habitat is not confined to a narrow linear belt as it is in the salt marsh. The fact that both adults assist in feeding the nestlings in both salt and fresh water marshes indicates, according to Armstrong's reasoning, that a harsh habitat exists. At the same time the maintenance of a smaller territory by Sapelo wrens implies a greater availability of food. However, a low rate of polygamy also indicates a harsh environment. These statements, I think, are contradictions.

Verner (1963a, 1964) in a comprehensive discussion of evolution of polygamy in avian mating systems, based on his study of two marsh wren populations in Washington, concluded that polygamy evolves in areas where population density is great enough that very marginal habitats are occupied. Females will mate with males that are already

mated in optimum habitat and ignore bachelor males in marginal habitats. If a polygamous male leaves more offspring with each additional female, then selection will favor polygamy. I shall show in Part II that population density of *griseus* in relation to the total optimum habitat is not so great that wrens are forced to occupy marginal habitat; thus the opportunity for polygamy is reduced. Several additional factors, discussed in Part II, also prevent the rise of a polygamous population. These are a high rate of nest mortality, small territory size, and the restriction of territories to narrow, linear bands along stream sides.

SONG

I have made no effort here to describe the song of *griseus*. Little is to be gained by adding still another interpretation of the Long-billed Marsh Wren song to those already attempted (Welter, 1935; Shufeldt, 1926-27; Saunders, 1926, and others). Once heard, the song is unforgettable. As Welter mentions, it is possible to distinguish between the call notes of the male and female. The call notes of fledglings (a location call and a begging call) differ from those of the adults.

The Long-billed Marsh Wren indulges in aerial song during the breeding season, as does also the Seaside Sparrow. Welter (1935) believed that the purpose of the flight accompanying the song is to check up on would be intruders. However, since song during flight occurs only during the breeding season, its function must be associated with territorial advertisement.

NIDIFICATION

Many hypotheses have been advanced to explain the intensive nest-building activity of male wrens. Welter (1935) discusses several of these hypotheses suggested in the literature (mock nests, practice nests, boundary markers, renestings, dormitories), but concludes that nest-building serves to utilize excess energy of an active bird restricted to a small area. Skutch (1940) also suggests that it is this restless energy that impels Central American wrens to build more nests than they actually need. However, Verner (1963a) states that "such an activity, requiring a great deal of time and energy and making the bird more conspicuous, would be selected against if it did not serve a very important function." He demonstrated that multiple nest building by males functions importantly in courtship. The male constructs several nests in a small courting center and delivers most of his songs from this area. Because of the small territory maintained by *griseus* I could rarely detect such courting centers within a territory. More often than not the entire territory functioned as the courting center.

EGG LAYING

A general conclusion that may be drawn from this study is that egg laying occurs any time between early April and mid-August, a four-month breeding season, but that no more than two broods are normally attempted by a female. In 1959 when egg laying began in early April, it ended in late July, and in 1958, when it began in late April, it ended in mid-August. The 1960 season was similar to the 1958 season, and the 1961 season began in late March, earlier than in the previous three years. Wayne (Sprunt and Chamberlain, 1949) gives the usual egg-laying period for *griseus* in the Charleston, S.C., area as "the last few days in June." In early seasons eggs were found in mid-May. Sprunt found eggs as early as 23 April. Because eggs have been found in July and as late as 9 August, the generalization is made that "Worthington's marsh wren raises three broods a season." This is, I think, an unsound conclusion drawn merely on the basis of finding eggs at late dates. In the case of *griseus* on Sapelo Island, where the breeding season begins somewhat earlier than in the Charleston area, a third brood is very rare, as previously mentioned.

Except in one instance I have not found a nest containing more than five eggs. This find was unusual in that the eggs appeared in an old nest. Three of them were very fresh while the other three were so old that they exploded when pricked with a pin. A plausible explanation is that the older three eggs were laid and then abandoned, and later the female, or another female, returned and began laying again.

E. Burnham Chamberlain (*in litt.*, 1958) advises me that of 28 full clutches of *griseus* examined in the previous seven or eight years in the Charleston, S.C., area by Ernest A. Cutts, only three, all in May, contained six eggs each. Cutts found that late season nests had no more than four eggs each, with a seasonal average of five.

Welter (1935) states that of 40 nests studied near Ithaca, N.Y., five eggs were the most frequent; extremes were 3-6. Other authors reviewed by Welter (Forbush in New England, Harlow in Pennsylvania and New Jersey) state that the average number is five, but clutch sizes vary from five to ten eggs per clutch. John W. Aldrich (personal communication, 1958) found an average of six eggs for the first brood in Ohio and five for the second brood. In Virginia, Bailey (1913) reported an average of five eggs per clutch, with six being a large set. Todd (1940) reported size of clutches in western Pennsylvania ranging from five to eight. Nicholson (Wheeler, 1931) reports that sets of *T. p. marianae* in Florida range from three to five, but sets of five are not as commonly found as smaller sets. Verner (1965) in Washington found clutch size for *T. p. paludicola* ranging from 4-6 eggs with a mean of five, and *T. p. plesius* from 5-8 eggs with an average of six.

It thus appears that the more northern races of *Telmatodytes palus-*

tris tend to have a wider range of clutch size and a higher average clutch size than do the southern races. Except for the three nests in the Charleston area, there are no reliable reports of clutches containing more than five eggs in any of the southern races. Lowery (*in litt.*, 1959) informs me that his statement in *Louisiana Birds* (Lowery, 1960) mentioning "five to nine eggs" is not based on a study of *T. p. thryophilus*, but is a generalization taken from the literature.

Skutch (1953) states that the Southern House Wren (*Troglodytes musculus*) in South America lays a usual set of four eggs and that "as with other wide ranging species, the clutch size increases with latitude until beyond the tropics, in Argentina, it may produce sets of nine eggs, a number which compares favorably with those known for the North American House Wren and the European Wren." In summary, then, I conclude that clutch size increases with latitude with the Long-billed Marsh Wren also.

Part II
POPULATION ECOLOGY AND BIOENERGETICS
POPULATION ECOLOGY

TERRITORY SIZE

The mean territory size in each study area is listed in Table 4. In the dissected areas along the Duplin River in 1958 (Area 1) the mean territory area was approximately 60 m². The measurements of these territories varied from 12-40 m in length and 1.5-3 m in width. In 1959 mean territory size of the Duplin River Area 4 was 110 m². However, Area 4, unlike the other study areas, contained patches of short grass (resulting from slumping of banks), which were not utilized by the wrens. The average utilized territory was estimated as 82 m².

In 1958 territories were more extensive in Area 2 than they were in 1959. Mean territory size in 1958 was 155 m² whereas in 1959 the mean size in the same study area was significantly less, being 85 m², or about one half the mean size in 1958 (Table 5). Territories 1-10 and 16-21 in 1959 occupied the same contiguous area that territories 1, 3-8, and 9-11 did in 1958. As shown in Table 5, the wrens defended larger territories on the same sites in 1958. Mean territory size in 1960 and 1961 in Area 2 was similar to mean size in 1959.

In 1958 the mean territory size of all territories under observation was approximately 110 m². In 1959-1961 the mean size was approximately 95 m², 90 m², and 100 m², respectively (Fig. 14). Ninety-eight territories, or almost 84% of the 116 territories measured, were less than 140 m² in area. Seventy-three territories, or approximately 63%, contained less than 100 m² of area.

Fig. 15 shows the linear arrangement of territories in the 1959 study areas. Owing to the small size of each territory and the total linear distance of each area, the individual territories are not drawn entirely to scale. Note that natural features such as small drainage channels often were recognized as boundaries by the wrens. The greater spacing of territories in Area 4 is due to the more extensive areas of short grass on the slumping levees.

Each territory with its area is listed in Appendix I. The size of the territory occupied by each pair of wrens varied considerably. However, within this area the wrens carry out all of their breeding activities. Rarely was an adult wren seen outside of its own territory during the breeding season.

TABLE 4
MEAN, STANDARD ERROR, STANDARD DEVIATION, AND COEFFICIENT OF
VARIATION OF TERRITORIES, 1958-1961

Year	Study Area	N	Mean & Standard Error (in m ²)	Standard Deviation	Coefficient of Variation (percent)
1958	1	11	60.0 ± 4.4	13.9	23.2
	2	12	155.8 ± 15.2	50.3	32.3
1959	2	22	85.3 ± 9.2	42.0	49.3
	4U ^a	18	82.2 ± 11.6	47.8	58.1
	4M ^b	18	106.6 ± 13.6	56.1	52.6
1960	2	14	96.9 ± 3.3	11.9	12.2
	4	13	88.0 ± 13.7	47.4	53.8
1961	2	15 ^c	90.7 ± 11.0	41.3	45.5
	4	11	112.8 ± 18.2	57.6	51.0

^a Utilized territory area.

^b Maximum territory area. In all other study areas, Utilized area = Maximum area.

^c 18 territories early in season, but three of these were annexed by males in adjacent territories by early June.

TABLE 5					
COMPARISON OF STUDY AREA 2 IN 1958 WITH STUDY AREA 2 IN 1959					
Year	N	Mean & Standard Error (in m ²)	Standard Deviation	V	Difference & S.E. Difference
a. All territories in Area 2, 1958 and Area 2, 1959.					
1958	12	155.75 ± 15.2	50.3	32.3%	70.4 ± 17.73 ^a
1959	22	85.33 ± 9.2	42.0	49.3%	
b. Same territory sites used by wrens in 1958 and 1959.					
1958	11	161.46 ± 15.4	48.5	30.1%	61.0 ± 18.36 ^b
1959	16	100.49 ± 10.1	39.1	38.9%	

^a Difference is significant at 0.99 level (t = 4.5; P < .01)

^b Difference is significant at 0.99 level (t = 3.3; P < .01)

NATALITY

Table 6 shows the potential and realized natality rates for 1958-1961. The maximum or physiological natality would be ten new wrens per pair of adults per year, since each pair theoretically could raise two broods per year from two 5-egg clutches.

MORTALITY

I recorded only three instances of adult mortality, two in 1959 and one in 1960. The carcass of a female covered with salt marsh ants (*Crematogaster clara*) was found on top of her nest on 14 May 1959. Close examination revealed that a small mammal (Rice Rat) had eaten most of the viscera and had chewed flesh from the bones. The second death was noted on 26 June 1959 when a female was found dead in an empty nest that had contained two eggs the previous week. The body had begun to deteriorate and the cause of death was not determined. On 28 June 1960 the carcass of a female was found on top of her nest in the same condition as the first dead female observed in 1959. Small shell fragments from the eggs of this female were inside the nest.

Data dealing with egg and nestling mortality were more complete than that dealing with adult mortality. Table 7 presents an analysis of loss of eggs and nestlings for 1958-1961. The total number of eggs laid each year is the basis for all percentages. Predation caused the greatest loss—39%, 67%, 67%, and 81% in 1958-1961, respectively. Each of the other agencies of importance, infertility and addling, desertion, and high tides caused considerably fewer losses. A summary of each agency follows.

Predation. In Tables 8 and 9 the loss of eggs and nestlings as a result of predation is analyzed for 1958-1961. Predation includes only nest losses that could be definitely attributed to animals. When a nest was robbed, but not damaged, the Rice Rat (*Oryzomys palustris*) was implicated. Rats may pull out and scatter some of the inner lining, but

TABLE 6
POTENTIAL AND REALIZED NATALITY RATES, 1958-1961

Year	MEAN NUMBER FEMALE NESTS/PR × YEAR	Potential Natality (Eggs/Pr × Yr)	Realized Natality (Eggs Hatched/ Pr × Yr)
1958	2.2	8.5	4.38
1959	2.6	10.3	3.73
1960	2.7	7.7	0.87
1961	2.5	9.6	1.83

TABLE 7						
ANALYSIS OF LOSS IN 266 NESTS, 1958-1961						
Agency	1958		1959		1960	
	No. Lost	% ^a	No. Lost	% ^a	No. Lost	% ^a
Predation						
Eggs	57	32.0	220	52.2	147	62.6
Young	13	7.3	62	14.7	10	4.2
Infertile or						
Addled Eggs	15	8.4	13	3.1	4	1.7
Desertion						
Eggs	8	4.5	25	5.9	9	3.8
High Tides						
Eggs	6	3.4	10	2.4	49	20.8
Young	4	2.2	5	1.2	0	0
Miscellaneous						
Young	1	0.6	0	0	0	0
Total Loss						
Eggs	86	48.3	268	63.6	209	88.9
Young	18	10.1	67	15.9	10	4.2
	104	58.4	335	79.5	219	93.1
					236	85.1

^a Percent total eggs: 1958 = 178; 1959 = 421; 1960 = 235; 1961 = 277.

the nest shows no other signs of disturbance. Large mammals were implicated when a nest was completely destroyed, knocked to the ground and robbed, or when the supporting grass stems were bent over and the nest robbed. Losses which could not be attributed to any particular animal, but were clearly caused by predation, are listed as undetermined predators.

In 1958 more predation was caused by large mammals (51%) than by Rice Rats (37%). In 1959 this picture changed considerably. Losses from Rice Rats accounted for approximately 84% of all predation, while losses from large mammals amounted to but 12%. In 1960 rat predation remained high (73%) and predation by large mammals increased slightly (18%). Percentage of loss by predators in 1961 was similar to that in 1958; 35% predation was caused by Rice Rats and 56% by large mammals.

The raccoon (*Procyon lotor*) and mink (*Mustella vison*) were probably the large mammals responsible for the predation on wren eggs and young. Both of these carnivores are commonly observed in and near wren habitats and I saw raccoon tracks around some of the destroyed nests. The extent of the damage to the nests clearly indicated activity of a large mammal. Although the mink is much less abundant in the marsh, the fact that it spends most or all of its time there indicates that it may be of importance as a predator. Mink build nests of dead *Spartina* on the ground on levees, or in hollow tree trunks that have been washed into the marsh by storm tides, and there give birth to their young (2-6 young/female have been observed). The young remain in the nest six to eight weeks or longer and thus a pair of mink may spend considerable time in and around wren habitat.

The River Otter (*Lutra canadensis*) is also present, but it is rarely seen and I never saw its tracks in my study areas.

In 1959-1961 I observed Rice Rats in almost every territory. They spent the daylight hours in male and female wren nests, and often built their own nests, especially later in the season, which to the untrained eye look similar to wren nests. Several litters of rats were found in old wren nests from early May to late July. No rats were seen during the breeding season of 1958. Predation by rats in 1958 was originally included in an undetermined predator category. The population density of Rice Rats was probably lower in 1958, when I saw none, than it was during the next three years when I noted so many.

Predation by animals that were not identified amounted to less than 5%, 3%, 2%, 3%, in 1958-1961, respectively. Suspects are Boat-tailed Grackles, Fish Crows (*Corvus ossifragus*), and Rice Rats. Fish Crows are often seen hunting over the marshes, and grackles occasionally nest in wren habitats.

Infertility and addling. Unhatched eggs in active nests were assumed to be infertile or addled. Unhatched eggs that disappeared shortly

TABLE 8						
ANALYSIS OF LOSS BY PREDATION IN 94 NESTS, 1958-1959						
Predator	No. Lost	1958 Percent Pred. ^a	Percent Total Eggs ^b	No. Lost	1959 Percent Pred. ^a	Percent Total Eggs ^b
Large Mammals ^c						
Eggs	28	40.0		24	8.7	
Young	8	11.4	20.2	9	3.2	7.8
Rice Rat (<i>Oryzomys</i>)						
Eggs	26	37.1		188	66.6	
Young	0	0	14.6	50	17.7	56.5
Undetermined						
Eggs	3	4.3		8	2.8	
Young	5	7.1	4.5	3	1.1	2.6
Total Loss						
Eggs	57	81.4		220	78.0	
Young	13	18.6		62	22.0	
Total	70		39.3	282		66.9

^a Percentage of total predation.

^b Percentage total number of eggs laid: 1958 = 178; 1959 = 421.

^c Raccoon and mink.

TABLE 9
ANALYSIS OF LOSS BY PREDATION IN 110 NESTS, 1960-1961

Predator	No. Lost	1960 Percent Pred. ^a	Percent Total Eggs ^b	No. Lost	1961 Percent Pred.	Percent Total Eggs
Large Mammals ^c						
Eggs	28	17.8	11.9	125	55.8	48.0
Young	0	0		8	3.6	
Rice Rat (<i>Oryzomys</i>)						
Eggs	115	73.2	53.2	78	34.8	30.3
Young	10	6.4		6	2.7	
Undetermined						
Eggs	4	2.5	1.7	7	3.1	2.5
Total Loss						
Eggs	147	93.6	66.8	210	93.7	80.8
Young	10	6.4		14	6.3	
Total	157			224		

^a Percentage of total predation.

^b Percentage total number of eggs laid: 1960 = 235; 1961 = 277.

^c Raccoon and mink.

after hatching of the brood were also considered to be in this category. Some adults removed unhatched eggs within a day or so after hatching of the brood, while others did not. Since it was not always possible to differentiate between infertility and addling, these causes were combined. Losses as a result of these causes were 8%, 3%, 2%, and 2%, in 1958-1961, respectively.

Desertion. In 1959 a female twice deserted when her nests were knocked over by a raccoon that had made a platform out of the marsh grass to which the nests were attached. These platforms, or ramps, are used by the raccoons to get above high water during the spring tides. (Fig. 16). They are constructed simply by bending the tops of *Spartina* to form a central mass or platform on which the animals can lie. In both of the instances cited above, the nests were not robbed by the raccoon.

Several cases of desertion were due to poorly attached nests. The nests had either completely fallen, or were twisted in such a manner that the entrance was upside down. I recorded no mortality due to desertion after the eggs hatched. Losses attributed to desertion in the study areas 1958-1961 were 4.5%, 5.9%, 3.8%, and 1.8%, respectively.

High tide water. Tide range at Sapelo Island varies from 1.4 to 3.2 m (4.5-10.5 ft) with a mean range of 2.06 m and a mean spring range of 2.42 m (Ragotzkie and Bryson, 1955). The tide is semidiurnal in character with an inequality in the range of tides daily, i.e., there is a higher high tide and a lower low, the other two tides being intermediate. The highest spring tide of the breeding season of 1958 occurred on 30 and 31 May. This was the only tide that inundated nests that year. In 1959 two periods of high spring tides occurred. The first was around 19 May, and the second 22 June. The latter period was accompanied by a northeasterly wind that increased the height of the predicted tides by approximately 0.6 m. In 1960 high spring tides accompanied by easterly winds occurred each month from April to early July, while no exceptionally high tides occurred in 1961.

Mortality (drowning) due to spring tides was relatively low in 1958 (6%) and 1959 (4%), considerably higher in 1960 (21%), and none at all in 1961 (0%). Area 1 in 1958 had a 16% drowning mortality. This same area was not kept under observation in 1959, but it was completely submerged during the spring tide of 22 June 1959 and the spring tides of 1960.

Miscellaneous causes. In 1958 a nestling disappeared from a nest between the time of hatching and prior to fledging. I presume that it died and was removed by one of the adults.

A possible mortality factor—not encountered in the study areas, but observed twice outside of them—is caused by rotting of the dead stems and continued growth of the green living stems to which the nest is

TABLE 10
SUMMARY OF NESTING SUCCESS, 1958-1961

	1958		1959		1960		1961	
	No.	% Eggs ^a	No.	% Eggs ^a	No.	% Eggs ^a	No.	% Eggs ^a
Females	21		41		30		29	
Nesting Attempts	46		108		62		53	
Eggs Laid	178		421		235		277	
Eggs Hatched	92	51.7	153	36.0	26	11.1	53	19.1
Egg Deaths	86	48.0	268	64.0	209	88.9	222	80.1
Young Deaths	18	10.0	67	16.0	10	4.2	14	5.0
Total Mortality	104	58.0	335	80.0	219	93.2	236	85.2
(Eggs + Young)								
Total Eggs Fledged								
(Nesting Success)	74	42.0	86	20.0	16	6.8	41	14.8

^a Percentage of total eggs laid.

attached. This causes the nest to slip and twist thus spilling out the eggs or young.

An uncommon, but possible, cause of mortality may occur later in the breeding season when nests are built in the tall grass along the outer edge of the levee. During high tides most of this outer grass stands in water. At this time, porpoises (the Atlantic Bottlenose Dolphin, *Tursiops truncatus*) or alligators (*Alligator mississippiensis*) have been observed to swim into the outer grassy area and to flatten tracts of tall grass. Why these animals do this is not known. Perhaps they are searching for fish. Some nests outside of the study areas have been destroyed in this manner (Fig. 17).

NESTING SUCCESS

In most bird population studies the major criterion for measuring reproductive "success" is the percentage of eggs laid that ultimately fledge, often termed "nesting success." The number of eggs fledged in 1958 was 74 out of a total of 178 laid, or a nesting success of 42% (Table 10). In 1959, 86 eggs fledged out of 421 laid, or a nesting success of only 20%. In 1960, 16 eggs fledged out of 235 laid, a nesting success of 7%. In 1961, 41 eggs fledged out of 277 laid, a nesting success of 15%.

FLEDGLING PRODUCTIVITY

Fledgling productivity is defined as the average number of fledglings produced per pair of breeding adults per year, and also per unit area. Productivity per pair of adults was calculated by dividing the total number of fledglings produced each year by the total number of pairs of breeding adults, regardless of whether or not every pair of adults had young that fledged.

Table 11 indicates that fledgling production was considerably less in 1959-1961 than it was in 1958. This is, of course, a direct result of the excessive predation that occurred during these three years. The figures of productivity in Table 11 might better be grouped under the term "nesting success productivity" to distinguish them from the total annual production listed in Table 23, which includes not only those young that fledged, but all of the eggs and young produced whether or not successfully fledged.

POPULATION TURNOVER RATE

The turnover rate for an animal population is the ratio between new material entering the system (production) and the amount present in the system. For birds the latter is the breeding stock or *standing crop*

TABLE 11				
ANNUAL FLEDGLING PRODUCTIVITY, 1958-1961				
Year	1958	1959	1960	1961
Utilized Habitat Area	2450 m ²	3860 m ²	2418 m ²	2610 m ²
No. of Adults (pr)	21	41	29	29
No. of Fledglings	74	86	16	41
Productivity				
Fledglings/pr $\times$ yr	3.50	2.15	0.55	1.41
Ash-free dry wt/pr $\times$ yr (gm)	9.34	5.74	1.47	3.76
Kcal/pr $\times$ yr	62.67	38.52	9.86	25.23
Fledglings/m ² $\times$ yr	0.030	0.022	0.007	0.016
Ash-free dry wt/m ² $\times$ yr (mgm)	80.6	59.5	18.0	42.0
Gcal/m ² $\times$ yr	540.8	399.2	118.5	281.4

TABLE 12				
POPULATION TURNOVER RATES, 1958-1961				
Year	1958	1959	1960	1961
Total Production (Grams dry biomass)	233	354	87	184
Initial Standing Crop	127	254	175	175
Turnover Rate	1.8	1.4	0.5	1.0

at the beginning of the breeding season. Table 12 shows turnover rates in the study areas for 1958-1961.

POPULATION DENSITY

The territory by territory census of nesting wrens in the Duplin River watershed in June of four consecutive years (1959-1962) indicated that 452, 453, 467, and 562 males were present, respectively. Assuming 4% unmated and 5% bigamous males, I estimated the total number of breeding pairs of wrens in the watershed at the peak of each breeding season as 457, 458, 471, and 568.

Table 13 shows density calculations from 1959 through 1962 in terms of three different areas as follows: (1) the number of pairs of wrens per total marsh area of the Duplin watershed excluding water area, i.e., crude density (Odum, 1959); (2) the number of pairs per tall *Spartina* streamside and levee marsh, i.e., potential or available wren habitat (specific or ecological density. Odum, op. cit.); and (3) the number of pairs per estimated area defended by male wrens, based on average territory size observed in the study areas. This is the utilized or "occupied area" density (Odum and Kuenzler, 1955). Mean territory size, 1959-1961, was 110 m², 95 m², 90 m², and 100 m², respectively. I made no measurements of territory in 1962, but observations suggested that the size was similar to sizes of the previous three years. Thus a mean of 100 m² was selected.

Density calculations (2) and (3) are of greater ecological significance than the crude density estimate because unsuitable and unused habitats are not included. The utilized area density indicates pressure the wrens place on local insect and spider food supply, while the difference between the utilized and ecological density indicates the degree of saturation of available habitat.

I made no attempts to census the winter population because the wrens tend to move throughout the marsh in all of the available tall and medium height *Spartina* habitat and into the areas of Black Rush that are between the *Spartina* marsh and the islands. At this time they move about in small groups and are very secretive. When "squeaked up" by hissing or kissing sounds the males rarely fly to the top of the

TABLE 13										
POPULATION DENSITIES OF ADULT MARSH WRENS IN THE DUPLIN RIVER WATERSHED, DURING THE BREEDING SEASONS 1959-1962										
Areal Basis	Hectares (Ha)	Area Acres (A)	Density-Pairs/hectare (Ha) or acre (A)							
			1959 (456 prs)		1960 (458 prs)		1961 (471 prs)		1962 (568 prs)	
			Ha	A	Ha	A	Ha	A	Ha	A
Crude Density (Total marsh less water area)	882		0.5		0.5		0.5		0.6	
		2190		0.2		0.2		0.2		0.2
Ecological Density (Potential habitat)*	10.1		45.1		45.3		46.6		56.2	
		25.0		18.2		18.3		18.8		22.7
Utilized Area Density (Mean territory size × number of territories)	**		101.1		109.0		98.1		99.6	
		**		41.7		44.9		40.6		41.2

* Based on census and aerial photo estimates.
 ** 1959 Area = 4.5Ha-10.9A; 1960 = 4.2Ha-10.2A; 1961 = 4.8Ha-11.6A; 1962 = 5.7Ha-13.8A.

grass as they readily do in the breeding season, but instead they tend to remain hidden in the grass and approach within a meter or so of the observer.

The data in Table 14 suggest that the majority of the wrens present in winter are the resident race, *T. p. griseus*. The northern races,

TABLE 14				
WINTER OCCURRENCE OF RACES ¹ OF <i>Telmatodytes palustris</i> COLLECTED IN SALT MARSHES OF SAPELO ISLAND, GEORGIA				
Date	Race ²			
	<i>griseus</i>	<i>waynei</i>	<i>palustris</i>	<i>dissaëptus</i>
18 Oct 1958	8	0	0	0
23 Oct 1959	7	1	0	0
29 Oct 1960	3	0	0	0
14 Nov 1958	5	1	0	1
1 Jan 1960	9	1	0	0
4 Mar 1961	6	4	1	0
4 Mar 1962	12	0	0	0

¹ Subspecific determinations made by T. D. Burleigh, United States National Museum, or by comparison with specimens determined by personnel of the National Museum.

² Breeding ranges (AOU Check-list, 1957).

- griseus*: Resident in coastal marshes from South Carolina to northern Florida.
- waynei*: Breeds in coastal marshes of southeastern Virginia and North Carolina.
- palustris*: Breeds in coastal and estuarine marshes from Rhode Island south to Virginia.
- dissaëptus*: Breeds from North Dakota east to New Brunswick, south to eastern Kansas, Indiana, south-central Pennsylvania and eastern Massachusetts.

waynei, *palustris*, and *dissaëptus*, are much less common, especially the latter two. All of these northern races have been collected at the WCTV tower in Leon County, Fla., by Herbert L. Stoddard during northward and southward migration, indicating that these races travel to wintering areas further south. While the influx of migrants in winter may increase the total population density (crude density), the ecological pressure in terms of food gathering per unit area is less in winter because the wrens utilize a larger area of the marsh. I noticed no differences in behavior during the winter season between the migratory and resident races in the salt marsh.

POPULATION BIOENERGETICS

BODY WEIGHTS AND ENERGY CONTENT

Table 15 is a summary of mean wing lengths and weights for wild *T. p. griseus* adults and immatures (see also Tables 43-45 in Appendix

TABLE 15
SUMMARY OF WING LENGTHS AND BODY WEIGHTS OF ADULT AND IMMATURE WRENS

		Wing length (mm)	Live Weight (gm)	Dry Weight (gm)	Fat Weight (gm)	Ash Weight (gm)	Ash-free Dry Weight (gm)
Adult males	N	34	52	41	35	39	39
	$\overline{M}$	48.2	10.61	3.61	1.03	0.37	3.26
	S.E.	± 0.3	± 0.1	± 0.05	± 0.04	± 0.004	± 0.05
	S.D.	1.7	0.7	0.3	0.23	0.02	0.3
Adult females	N	19	25	24	18	21	21
	$\overline{M}$	45.2	9.41	3.12	1.04	0.33	2.86
	S.E.	± 0.5	± 0.22	± 0.10	± 0.06	± 0.007	± 0.10
	S.D.	2.1	1.1	0.5	0.26	0.03	0.4
Immatures	N	34	56	35	34	34	34
	$\overline{M}$	45.6	9.44	3.23	1.04	0.30	2.94
	S.E.	± 0.4	± 0.21	± 0.07	± 0.04	± 0.006	± 0.06
	S.D.	2.1	1.6	0.4	0.21	0.04	0.4

TABLE 16			
MEAN WET, DRY, AND ASH WEIGHTS OF MARSH WREN EGGS			
Days Incubated	N	Mean & Standard Error (gm)	Standard Deviation
Fresh-2 days			
Wet Wt.	68	1.17 ± 0.01	0.10
Dry Wt.	53	0.28 ± 0.003	0.22
3-8 days			
Wet Wt.	41	1.11 ± 0.01	0.07
Dry Wt.	30	0.26 ± 0.005	0.01
9-13 days			
Wet Wt.	18	1.06 ± 0.02	0.08
Dry Wt.	7	0.24 ± 0.002	0.008
All eggs 1-13 days			
Wet Wt.	127	1.14 ± 0.01	0.10
Dry Wt.	90	0.27 ± 0.003	0.02
Ash Wt.*	27	0.10 ± 0.002	0.008
Egg Shell			
Dry Wt.	35	0.09 ± 0.003	0.20

* Ash as % dry weight of eggs = 35.4%. Mean ash-free dry weight (mean dry weight minus mean ash weight) = 0.1749 gm.

TABLE 17			
MEAN WET AND DRY WEIGHTS OF MARSH WREN NESTLINGS AND FLEDGLINGS			
Age	N	Mean & Standard Error (gm)	Standard Deviation
Nestlings			
0-5 Days			
Wet	21	1.38 ± 0.08	0.36
Dry	17	0.22 ± 0.02	0.06
Mean ash weight = 0.030 gm, Ash —% Dry Wt = 11.4%			
5-9 Days			
Wet	9	5.69 ± 0.77	2.19
Dry	8	1.09 ± 0.20	0.53
Mean ash weight = 0.131 gm, Ash —% Dry Wt = 8.5%			
9 Days to Fledgling			
Wet	23	8.42 ± 0.16	0.75
Dry	7	2.58 ± 0.18	0.43
Mean ash weight = 0.219 gm, Ash —% Dry Wt = 8.8%			
Fledglings			
Wet	5	8.84 ± 0.35	0.70
Dry	5	2.92 ± 0.16	0.32
Mean ash weight = 0.247 gm, Ash —% Dry Wt = 8.5%			

TABLE 18		
MEAN WING LENGTHS AND BODY WEIGHTS OF FIVE CAPTIVE ADULT WRENS		
	Males (3)	Females (2)
Wing length	49.5 mm	46.6 mm
Live (wet) Weight	11.08 gm	9.85 gm
Dry Weight	3.96	3.39
Fat Weight	1.31	1.19
Ash Weight	0.36	0.27
Ash-free Dry Weight	3.60	3.12

II). Adult males (10.61 ± 0.10 gm) are significantly heavier than adult females (9.41 ± 0.22 gm) at the 0.99 level ($P < .01$). There is a tendency for immature males (9.68 ± 0.25 gm) to be slightly heavier than immature females (9.10 ± 0.24 gm), but the differences are significant only at the 0.50 level ($.50 > P > .10$). Mean body weight of the immatures (9.44 ± 0.21 gm) is similar to that of adult females.

Weight data on eggs, nestlings, and fledglings are presented in

TABLE 19					
COMPARISON OF (S) SPRING (MARCH TO SEPTEMBER) AND (W) WINTER (SEPTEMBER TO MARCH) WEIGHTS OF CAPTIVE WRENS					
Wren No.	Season	N	Mean & S.E. (gm)	S.D.	Significance
12 m	W	8	10.3 ± 0.2	0.5	$P < .01$
	S	12	11.7 ± 0.2	0.7	
84 m	W	16	9.6 ± 0.1	0.4	$P < .01$
	S	42	10.0 ± 0.1	0.4	
85 m	W	18	10.1 ± 0.2	0.7	$P < .01$
	S	44	10.8 ± 0.1	0.5	
86 m	W	19	9.4 ± 0.1	0.4	$P < .01$
	S	18	9.8 ± 0.1	0.4	
87 m	W	23	10.7 ± 0.1	0.5	$P < .01$
	S	34	11.9 ± 0.1	0.6	
92 m	W	23	10.4 ± 0.1	0.4	$P < .01$
	S	34	11.9 ± 0.1	0.6	
98 m	W	17	9.4 ± 0.1	0.5	$P < .01$
	S	34	10.0 ± 0.1	0.4	
11 f	W	11	8.4 ± 0.2	0.7	$.05 > P > .02$
	S	11	9.0 ± 0.2	0.5	
83 f	W	19	8.8 ± 0.1	0.2	$.10 > P > .05$
	S	21	9.1 ± 0.1	0.4	
91 f	W	18	9.2 ± 0.1	0.5	$.10 > P > .05$
	S	24	9.6 ± 0.2	0.8	

TABLE 20
MEAN ENERGY CONTENT OF MARSH WREN TISSUE

	N	Kilocalories/gram			
		Per ash-free		Per ash-free	
		Lean-Dry Weight	S.D.	Dry Weight*	S.D.
		Mean $\pm$ S.E.		Mean $\pm$ S.E.	
Lipids extracted prior to combustion					
Adults & Immatures	26	5.33 $\pm$ 0.06	0.29	6.60 $\pm$ 0.14	0.22
Fledglings	3	5.15 $\pm$ 0.05	0.07	6.71 $\pm$ 0.13	0.19
Experimental Adults	5	5.36 $\pm$ 0.07	0.14	6.70 $\pm$ 0.09	0.18
Whole Wrens Combusted					
Adults	8			6.17 $\pm$ 0.09	0.20
Nestlings	23(7)**			6.13 $\pm$ 0.21	0.16
0-5 days	16(2)			5.98	
5-9 days	4(2)			6.15	
9-13 days	3(3)			6.22	
Eggs (1-13 days)	64(5)			6.74 $\pm$ 0.08	0.16

* Includes caloric value of the extracted fat = 9.0 Kcal/gram.

** Number in brackets = number of pooled samples combusted.

Tables 16 and 17. Weights of five of the captive (experimental) wrens are summarized in Table 18.

Captives increased in weight in the spring. For the captive males (Table 19) the differences between winter and spring are significant at the 0.99 level ($P < .01$) and for the females significant at the 0.90–0.98 level ($P < .10$ to $P > .02$). A comparison of weights of 14 wild adult males collected from October through March with weights of 38 adult males collected April through August follows the same trend although the difference is significant only at the 0.50 to 0.90 level ($0.50 > P > 0.10$).

Mean caloric values of wild adults, immatures, fledglings, nestlings, and eggs, and of captives are shown in Table 20. There is a significant difference in results of the two methods based on whole and fat-extracted birds. The reason for this is not fully understood; however, the two groups of wrens did not receive the same drying treatment prior to burning. Whole birds were dried to constant weight at 100°C

TABLE 21
ENERGY CONTENT (KCAL/GM ASH-FREE DRY WEIGHT) OF
NATURAL FOOD OF *T. p. griseus*

	Kcal/gm	Ordinal Mean
Mixed Hymenoptera	5.76	
Marsh Ant	6.50	6.13
(<i>Crematogaster clara</i>)		
Mixed Diptera	5.46	
<i>Chaetopsis aenea</i> (Otitidae)	5.60	5.52
<i>Chaetopsis apicalis</i> (Otitidae)	5.21	
Hemiptera		5.63*
<i>Ischnodemus badius</i>	5.63	
<i>Trigonotylus</i> sp.	5.30	
Homoptera		5.38
<i>Prokelisia marginata</i>	5.38	
Orthoptera		5.62
<i>Orchelimum fidicinum</i> -Adults	5.45	
<i>Orchelimum fidicinum</i> -Nymphs	5.64	
<i>Orchelimum fidicinum</i> -Mixed	5.78	
Mixed Coleoptera	5.81	5.81
Lepidoptera larvae	5.17	5.17
Miscellaneous insect mixture	5.52	
Spiders (several species)	5.62	5.62
Molluscs (<i>Littorina irrorata</i>)**	4.19	4.19
Arthropoda (<i>Uca</i> . sp.)***	5.1	5.1

* *I. badius* comprises 99% of all hemiptera eaten.

** Data from Smalley (1959).

*** Data from Sharp (1962).

and stored for a considerable length of time, while the extracted wrens were vacuum dried at 40° prior to extraction. There was possibly some loss of fat from the whole birds during the grinding process.

The caloric content in Kcal/gm ash-free dry weight of various natural food items of wrens is listed in Table 21. For purposes of making estimates of the caloric value of insect and spider standing crops, per square meter of marsh habitat, a mean caloric value for each group was calculated.

POPULATION BIOMASS

Estimated standing crops of adult wrens in the Duplin River watershed in June of each year, 1959-1962, are listed in Table 22 in terms of density (numbers), biomass (ash-free dry weight) and energy (gcal) per square meter of potential habitat (ecological density) and per square meter of occupied area (occupied or utilized area density). The standing crop of adults per square meter of habitat was very similar at the beginning of each breeding season, and did not reflect the previous season's production of young in any way.

Estimated changes in biomass, including adults, eggs, and young during the breeding season in the special study areas are graphed in Fig. 18. Details of these data are summarized by census periods in Table 58 and 60 in Appendix IV. The censuses upon which Fig. 18 was based began with the week prior to the first egg laying and ended with the week after the last nestling was fledged. Start of breeding varied somewhat each year depending on the severity of weather conditions in February and March. The year 1960 was an extremely poor one for the wrens. The combination of high spring tides each month from April to early July and increased predation by Rice Rats greatly reduced production. Wren fledglings were not seen or heard in the marsh until 15 July 1960, whereas in the previous two years and in 1961 fledglings were observed by mid-May.

Production of new wren biomass at weekly intervals in gram calories per square meter in the study areas from 1958 through 1961 is shown in Table 60 in Appendix IV. A summary of annual production of new wren biomass is presented in Table 23. Production for each year from 1958 through 1961 in gcal/m² × yr. was 589, 569, 230, and 441, respectively.

ENERGY REQUIREMENTS

Feeding experiments. Metabolism of marsh wrens determined by feeding experiments is summarized in Table 24. Means (in Kcal/gm ± S.E.) of all determinations were: Mean daily energy intake = 11.55 ± 0.1; excretory energy loss = 2.7 ± 0.03; assimilated, or available

TABLE 22
NUMBERS, BIOMASS (MILLIGRAMS ASH-FREE DRY WEIGHT) AND ENERGY CONTENT IN AN ADULT
POPULATION OF WRENS IN JUNE OF EACH YEAR 1959-1962 (P) = POTENTIAL HABITAT,
(O) = OCCUPIED HABITAT

Year (Habitat)	1959		1960		1961		1962	
	(P)	(O)	(P)	(O)	(P)	(O)	(P)	(O)
Total number of wrens		912		916		942		1136
Density per square meter	0.009	0.020	0.009	0.021	0.009	0.019	0.011	0.020
Biomass per square meter (mgm)	27.6	62.0	27.7	66.7	28.5	60.0	34.4	60.9
Energy per square meter (gcal)	182.3	409.3	183.1	440.4	188.3	396.2	227.1	402.4

TABLE 23										
ANNUAL PRODUCTION OF WREN BIOMASS IN GRAMS ASH-FREE DRY WEIGHT AND KILOCALORIES, 1958-1961										
	1958			1959			1960			1961
	N	Gm	Kcal	N	Gm	Kcal	N	Gm	Kcal	Gm
Eggs	86	15	101	268	47	316	209	36	246	41
Young										
1 Day	2	1	3	6	1	7	2	1	3	0
5 Day	13	12	84	49	47	288	8	8	47	0
10 Day	3	7	44	9	21	130	0			14
Pre-fledged	0			3	8	49	0			0
Fledged	74	198	1211	86	230	1407	16	43	262	110
Total Production		233	1443		354	2197		87	555	184
Total Area			2450m ²			3860m ²			2418m ²	2610m ²
Production per m ² yr		95mgm	589gcal		92mgm	569gcal		36mgm	230gcal	70mgm
										441gcal

metabolized energy = 8.8 ± 0.1 . For a mean body weight of 10.0 gm, mean assimilated energy was 37 gcal/gm $\times$ hr. Only a small part of the metabolized energy was stored as fat or put into reproductive organs. The largest weight gain by an individual wren during any period was 1.2 gm. This same wren had lost 1.4 gm, the largest loss by an individual, the previous week. Weight gains and losses were relatively small most of the time. The energy remaining after accounting for storage or gains from fat catabolism is the energy expended in body maintenance and activity (respiration) or the existence energy. This value was 8.8 ± 0.1 Kcal/day or 37 gcal/gm $\times$ hr. This value is the same value that was found for the assimilated energy, indicating that essentially, catabolism balanced anabolism as would generally be expected in non-migratory adult birds.

Data pertaining to energy content of individual wrens, wren food (mealworms and wren mixture), and wren feces are listed in Appendix II (Tables 46-51).

Average assimilation efficiency (digestive efficiency or coefficient) for the experimental wrens on the mealworm-wren mixture diet was $75.9 \pm 0.5\%$ (range: 73.5-78.3) and showed small variation (coefficient of variation = 8%).

Feces of confined birds were quite uniform in appearance and contained no identifiable particles. Most of the wrens ejected by mouth several times weekly a small pellet composed of skin and jaws of mealworm larvae. I added these pellets to the feces during periods of energy measurements. Feces from adults found in nests usually contained undigested chitinous fragments of insects and spiders. Thus the assimilation efficiency of wild wrens may be somewhat lower than that of confined wrens, but energy content per gram ash-free dry weight of feces from wild birds was found similar to that of the captive wren feces.

Gibb (1957) found that assimilation efficiency of a nestling Coal Tit (*Parus ater*) on a diet of mixed insects consisting of caterpillars, weevils, hemiptera, and spiders was approximately 67%. Assimilation efficiency by adults is generally higher than it is for nestlings based on comparisons of adult and nestling feces of several species of birds (personal observation). Efficiency of food utilization has been shown to increase from low to high temperatures (Kendeigh, 1949; Seibert, 1949; Davis, 1955; West, 1960) and from short to long photoperiods (Cox, 1961), and appears to be related to the speed of movement of food through the intestinal track. At higher temperatures or longer photoperiods a higher efficiency can be maintained as a result of a lower feeding rate, which allows food to be digested more completely (Cox, op. cit.). Variation in assimilation efficiencies over a wide range of temperatures is generally less than 10%, often less than 5%. Individual variation may be greater for a particular species at a single

TABLE 24

MEANS (IN KILOCALORIES) OF 173 WEEKLY DETERMINATIONS OF DAILY INTAKE, LOSS, ASSIMILATION, AND RESPIRATION (EXISTENCE ENERGY) OF 10 CAPTIVE WRENS. (C.V. = COEFFICIENT OF VARIATION, A/I (ASSIMILATION/INTAKE) = ASSIMILATION EFFICIENCY)

	Mean Weight (grams)	Gross Intake	Excreta Loss	Assimilation		Respiration*		A/I (%)
				Day	Gm/Hr	Day	gm/hr	
$\bar{M}$	10.0	11.55	2.7	3.8	0.037	8.8	0.037	75.9
S.E.	± 0.1	± 0.1	± 0.03	± 0.1	± 0.0004	± 0.1	± 0.0003	± 0.5
S.D.	1.0	1.3	0.40	1.0	0.005	0.9	0.004	6.2
C.V.	9.9%	11.3%	16.2%	10.9%	13.9%	10.7%	11.5%	8.1%

* Existence energy. All but a small fraction of assimilated energy was respired.

TABLE 25 COMPARISON OF RESPIRATION (EXISTENCE ENERGY) IN GOAL/GM X HR BY FIVE CAPTIVE WRENS (N = NUMBER OF WEEKLY MEASUREMENTS)						
Wren No.	N	Breeding and Molt Periods	Non-breeding, Non-molt Periods		Significance of Difference	P
		Mean & Standard Error	Mean & Standard Error	Difference ± S.E.		
85m	6	35.7 ± 0.5	31.3 ± 1.7	4.38 ± 1.18	3.71	P < .01
86m	6	41.8 ± 0.8	39.7 ± 1.0	2.18 ± 1.40	1.56	.5 > P > .1
98m	6	36.0 ± 0.8	34.2 ± 0.9	1.83 ± 1.49	1.23	.5 > P > .1
92m	9	36.7 ± 0.7	36.6 ± 0.9	0.15 ± 1.12	0.13	P > .5
83f	8	38.8 ± 0.1	36.4 ± 0.8	2.42 ± 1.48	1.63	.5 > P > .1

temperature, than variation for the species as a whole over a range of temperatures. Because the major portion of the breeding season of *griseus* occurs within its thermoneutral zone (see below), I have assumed an assimilation efficiency of 70% for the purposes of this study.

Since energy measurements were conducted during periods of song and courtship (in males) and during periods of molt (two complete molts each year by both sexes) as well as during non-breeding, non-molt periods, the mean values for existence energy listed in Table 24 include these extra energy-requiring activities.

Individual differences proved to be greater than mean seasonal differences for the group as a whole. A comparison of metabolism by each individual during one period with its metabolism at another did reveal differences between spring-summer and autumn-winter periods (Table 25). In only one instance (Wren 85 ♂) was the difference significant at the 99% level. During periods of courtship and molt this male expended 15% more energy than during seasons when these activities were absent. Differences in metabolism between the two periods were not highly significant in the other individuals, although three wrens did exhibit slightly greater metabolism during breeding-molt periods ($P > 0.1$). In wild birds an increase in energy requirements during molting and breeding would be expected (Kendeigh, 1941, 1963a, b, and Kendeigh, Krammer and Hamerstrom, 1956). The experimental wrens were confined to their cages and thus many of their breeding activities were restricted. Singing, displaying, and tearing of strips of paper from the floor covering (newspaper was placed on floors of cages when metabolism was not being measured) was the extent of courtship activity by these males.

Although mean respiration rate for females ($40 \text{ gcal/gm} \times \text{hr.}$) appears slightly higher than the rate for males ($37 \text{ gcal/gm} \times \text{hr.}$), a T-test indicated the difference is not significant. Therefore metabolism values of both sexes have been combined in Table 24.

Oxygen consumption. Data on the relation of oxygen consumption under near standard conditions (post absorption in the dark) to ambient temperatures are summarized in Fig. 19 and Table 26. Metabolic rates of more active wrens not in a post absorptive state are summarized in Table 27 and are indicated on Fig. 19 by open circles.

Because only a few individuals were used for determinations of oxygen consumption at temperatures above 35°C , and below 20°C , no regression line has been fitted to the points. However, means (± 2 standard errors) of the near basal values for each 5° interval (10° interval from 5 - 15°C) from 5° to 45°C are indicated by the line connecting the mean values for each interval. Means ($\pm 2 \text{ S.E.}$) of the higher metabolic rates of the active wrens are shown for the intervals between 20° and 30°C .

The metabolic data presented in Fig. 19 indicate that the thermo-

TABLE 26
MEAN OXYGEN CONSUMPTION IN ML/GM X HR UNDER STANDARD OR NEAR-BASAL CONDITIONS

Temperature Interval °C	5-15*	15-20	20-25	25-30	30-35	35-40	40-45
No. of Deter- minations	4	7	12	14	4	3	5
Mean	8.9	7.0	4.9	4.6	4.6	7.0	7.1
S.E.	± 0.7	± 0.6	± 0.05	± 0.3	± 0.4	± 0.9	± 0.3
S.D.	1.2	1.4	0.2	0.9	0.6	1.3	0.6
V.	13.7%	19.5%	3.4%	19.8%	14.1%	18.7%	7.9%
2 S.E.	± 1.4	± 1.1	± 0.1	± 0.5	± 0.8	± 1.8	± 0.6

* First interval = 10°C, all others = 5°C.

TABLE 27
 BODY WEIGHTS, OXYGEN CONSUMPTION, AND HEAT PRODUCTION OF ACTIVE MARSH
 WRENS AS DETERMINED BY OXYGEN RESPIROMETRY
 (MEAN $\pm$ S.E.)

Wren No.	N*	Weight (gm)	Ce O ₂ / gm $\times$ Hr	Kcal/bird $\times$ day
87m	6	11.20 $\pm$ 0.21	6.8 $\pm$ 0.5	9.0 $\pm$ 0.4
92m	4	10.64 $\pm$ 0.66	5.8 $\pm$ 0.2	7.3 $\pm$ 0.4
84m	4	9.63 $\pm$ 0.22	7.4 $\pm$ 0.8	8.4 $\pm$ 0.9
85m	1	9.85	6.7	7.8
86m	2	9.43	8.8	7.9
12m	1	12.12	5.9	8.5
91f	2	9.20	8.5	7.8
83f	3	9.17 $\pm$ 0.05	6.3 $\pm$ 0.2	6.8 $\pm$ 0.3
11f	5	8.66 $\pm$ 0.17	8.2 $\pm$ 0.3	8.4 $\pm$ 0.5
Mean		9.94 $\pm$ 0.22	7.04 $\pm$ 0.22	8.21 $\pm$ 0.22

* N = number of determinations.

neutral zone for the marsh wren lies between 23° and 35°C. Above or below this zone the rate of oxygen consumption rose significantly. One male, represented by the point at 38.5° died at this temperature, and a second male died at 45°C.

I found no differences in a comparison of weight-specific oxygen consumption.

The lowest values of metabolism of post absorptive wrens resting in the dark (but not at night) at temperatures within the zone of thermoneutrality are listed in Table 28 and are similar to the mean BMR (basal metabolic rate) of common Redpolls (*Carduelis f. flammea*),

TABLE 28
 MINIMAL LEVELS OF METABOLISM OF MARSH WRENS IN
 THERMONEUTRAL ZONE AS DETERMINED IN
 OXYGEN RESPIROMETER

Wren No.	Weight (gm)	T _A (°C)	Metabolism		
			MI O ₂ / gm $\times$ Hr	Kcal/ gm $\times$ Hr	Kcal/ bird $\times$ day
86m	8.94	26°	3.0	0.015	2.82
92m	10.91	27°	3.3	0.016	4.23
84m	9.82	27°	3.7	0.018	4.23
87m	11.58	23°	4.1	0.020	5.68
85m	11.54	28°	4.2	0.021	5.68
91f	8.54	27°	4.2	0.021	4.25
83f	9.34	31°	3.8	0.019	4.23
Mean	10.10		3.8	0.018	4.44

weight 10.3 gm, which was reported by Steen (1958) as being 4.6 ml/gm $\times$ hr., and somewhat lower than the BMR of 5.2 ml/gm $\times$ hr. reported by Kendeigh (1939) for House Wrens (average weight 11.1 gm).

Production of carbon dioxide. Production of carbon dioxide by wrens that were not in a post absorptive state but were resting quietly in a dark box, within the thermoneutral zone, is shown in Table 29. Oxygen consumption by the same wrens determined within a day or

TABLE 29				
RELATION OF PRODUCTION OF CARBON DIOXIDE TO OXYGEN CONSUMPTION BY CAPTIVE WRENS				
Wren No.	Weight (gm)	Carbon dioxide Production cc/gm $\times$ hr	Oxygen Consumption cc/gm $\times$ hr	R.Q.
Inactive Wrens				
86m	10.05	4.0	5.1	0.78
12m	11.54	3.8	4.8	0.77
87m	12.77	3.7	4.1	0.90
92m	11.65	4.0	4.5	0.88
83f	9.11	5.6	5.9	0.93
			mean	0.85
Active Wrens				
86m	10.05	6.7	6.8	0.98
12m	11.54	5.2	5.9	0.88
87m	12.77	6.9	7.0	0.98
92m	11.65	5.4	5.4	1.00
83f	9.11	6.6	6.5	1.00
11f	9.56	7.4	8.1	0.90
			mean	0.96
				mean both groups: 0.90

so of the CO₂ determinations, under the same conditions and on the same diet, are also listed in Table 29. The CO₂ consumption of these wrens while unrestrained in the respirometer was also determined (Table 29). From these data a mean respiratory quotient (RQ) was computed for both groups of measurements. The thermal equivalent of the observed oxygen consumption was calculated by the equation (see King and Farner, 1961): Kcal/liter O₂ = 3.815 + 1.232 RQ. Thus heat production at an RQ of 0.85 is 4.86 Kcal/liter O₂, and at an RQ of 0.96 it is 4.99 Kcal/liter O₂, or a mean caloric value of 4.93 Kcal/liter of oxygen.

Relation of metabolism to body weight. The relation of metabolism in kilocalories per day to body weight is illustrated in Fig. 20. Solid circles represent wrens in basal or near basal conditions, while open

TABLE 30					
SUMMARY OF METABOLISM AS DETERMINED BY OXYGEN RESPIROMETRY					
Near-basal Conditions			Light Activity		
Weight (gm)	Ce O ₂ / gm × hr	Kcal/bird × day	Weight (gm)	Ce O ₂ / gm × hr	Kcal/bird × day
N	30	30	28	28	28
$\overline{M}$	10.4	5.8	9.94	7.04	8.2
S.E.	± 0.2	± 0.2	± 0.2	± 0.2	± 0.2
S.D.	1.2	1.2	1.1	1.2	1.2
C.V.	11.3%	21.3%	11.4%	16.4%	14.2%

circles indicate more active birds. The slopes of the King-Farner (1961) Equation

$$\log M = \log 74.3 + 0.774 \log W (\text{Kg})$$

and the Brody-Proctor Equation (cfn. King and Farner, op. cit.)

$$\log M = \log 89 + 0.64 \log W$$

have been drawn on the figure to indicate the relationship of the wren data to the levels of standard metabolism predicted for birds of this size range by the two equations. The minimal levels of metabolism of marsh wrens are close to those predicted by the King-Farner Equation, although since many of the determinations were not conducted under rigorous basal conditions, they are slightly higher. Practically all of the near basal determinations, however, are lower than basal levels predicted by the Brody-Proctor Equation. Similarly, Lasiewski (1963) has noted that basal metabolism of hummingbirds is close to, or identical with, the King-Farner Equation predictions.

Metabolism of wrens in terms of oxygen consumption (cc. $\text{O}_2/\text{gm} \times \text{hr}$) and heat production (Kcal/bird $\times$ day) as measured by the oxygen respirometer is summarized in Table 30.

POPULATION RESPIRATION

In order to estimate adequately the energy flow of the wren population one must know the respiration rates of each age component of the population at temperatures of the natural environment. Monthly mean temperatures for the years 1958-1961 (Table 57, Appendix III) indicate that the period from May through September and including, possibly, October are within the thermoneutral zone of wren metabolism. Thus the value of 8.8 Kcal/bird $\times$ day, as determined by feeding experiments within this zone was considered the minimum daily respiration of an adult during this period. Respiration during the early part of the breeding season (March through April), when the mean monthly temperatures are below 22°C , was estimated at approximately 11 Kcal/bird $\times$ day based upon oxygen consumption measurements of wrens at temperatures between 5° and 20°C .

Uramoto (1961) suggests that wild birds require approximately 30% more energy than captive birds do. Thus the respiration values of *griseus* would be 10.6 Kcal/bird $\times$ day during the summer months. However, the captive wrens were extremely active in their cages and hopped or flew incessantly. Therefore no correction factor was added to the respiration estimates listed in Table 31.

I made no direct measurements of respiration of nestlings or fledglings. However, the studies of Kendeigh (1939) on young House Wrens and those by Dawson and Evans (1957, 1960) on nestling

TABLE 31
ENERGY FLOW (ASSIMILATION) AND RESPIRATION (VALUES IN
PARENTHESES) IN GCAL/M² × DAY, 1958-1961

Week	1958	1959	1960	1961
Mar. 27-Apr. 3		219 (219)		249 (249)
Apr. 4-10		220 (219)		249 (249)
Apr. 11-17	198 (198)	222 (219)		249 (249)
Apr. 18-24	198 (198)	221 (219)	264 (263)	249 (249)
Apr. 25-May 1	201 (198)	236 (232)		254 (249)
May 2-8	160 (158)	249 (230)	212 (211)	203 (200)
May 9-15	199 (189)	249 (236)		206 (202)
May 16-22	218 (207)	270 (267)		222 (214)
May 23-29	237 (233)	270 (263)	213 (211)	233 (224)
May 30-Jun. 5	250 (241)	257 (255)		226 (223)
Jun. 6-12	265 (255)	275 (268)	215 (211)	234 (228)
Jun. 13-19	252 (250)	291 (282)	216 (211)	232 (230)
Jun. 20-26	259 (254)	300 (292)	207 (204)	233 (230)
Jun. 27-Jul. 3	265 (258)	311 (304)	198 (196)	235 (232)
Jul. 4-10	269 (266)	307 (305)	202 (199)	241 (237)
Jul. 11-17	263 (262)	319 (315)	203 (200)	259 (251)
Jul. 18-24	272 (264)	315 (310)	198 (197)	267 (260)
Jul. 25-31	266 (264)	318 (316)	209 (204)	265 (263)
Aug. 1-7	272 (268)	315 (314)	222 (217)	278 (273)
Aug. 8-14	290 (280)	307 (305)	229 (227)	284 (281)
Aug. 15-21	301 (297)		247 (240)	273 (273)
Aug. 22-28	308 (302)		235 (232)	

Field (*Spizella pusilla*), Chipping (*S. passerina*), and Vesper Sparrows (*Pooecetes gramineus*) indicate that respiration rate by very young altricial nestlings during the first half of their nestling life is relatively low, ranging from 10-20 gcal/gm × hr. The major portion of the energy intake is converted into new biomass, because temperature regulation is not functional until the fifth or sixth day (Kendeigh, 1928, 1939; Odum, 1942). After this age respiration by young birds approaches or surpasses that of adults. Dawson and Evans (1957) state that in approximately five days nestlings

“are transformed from passive creatures capable principally of ingestion, digestion, and ejection into active young birds capable of standing, moving about, and attempting to fly. These changes in behavior are accompanied by an increased intensity of metabolism during the nestling period probably owing principally to the relatively greater proportion of muscle present and to increased motor activity.”

The data from Kendeigh (1939) and Dawson and Evans (1957, 1960), indicate that at above five days of age nestling metabolism

ranges from 20 to 40 gcal/gm. $\times$ hr. depending upon activity while fledgling metabolism is similar to adult metabolism. On this basis metabolism of nestlings 1, 5, and 10 days of age were estimated at approximately 0.5, 2.7, and 5.0 Kcal/bird $\times$ day, respectively. Fledgling metabolism was considered to be approximately 7.6 Kcal/bird $\times$ day. Total estimated respiration in gcal/m² of standing crop of nestlings at weekly intervals is shown in Appendix IV, Table 61).

I omitted metabolism of developing embryos within incubated eggs from the energy flow calculations. Egg respiration is probably low because the egg receives most of its heat income from the brooding adult and converts a large part of its biomass and energy into new tissue. Mean weight changes of eggs from a mean fresh weight of 1.174 ± 0.012 gm to a mean prehatching weight of 1.064 ± 0.019 gm indicate a mean loss of only 0.110 gm, some of which is probably water.

Total respiration, in gcal/m² $\times$ day, of the standing crop of wrens at weekly intervals during the breeding season is presented in Table 31.

POPULATION ENERGY FLOW

The total population assimilation rate, or energy flow (Table 31), during the breeding season was obtained by adding production (Table 60) to respiration (values in parentheses in Table 31), and is graphically depicted in Fig. 18. Daily respiration comprised most of the energy flow so it is not shown as a separate curve in Fig. 18.

DENSITY OF INSECTS AND SPIDERS

Estimated density, dry biomass, and caloric content of insects and spiders per square meter of marsh are shown in Table 32 for ten one-square-meter quadrat bag samples collected in occupied wren territories. By this method are collected the insects and spiders that live in the leaf crevices and stems, as well as those that are sedentary or slow flying, such as fulgorids, but almost none of the more active flying hymenoptera and diptera. Analyses of the removal sweep samples, which were collected chiefly by other investigators, are incomplete; however, preliminary estimates indicate that this method collects the active flyers (from 5-300 individuals/m²). The high densities in several of the bag samples resulted from the presence of several dead stems of *Spartina* containing ant colonies (*Crematogaster clara*) in the 4 March and 14 June samples, and a very high concentration of adults and nymphs of the marsh fulgorid (*Prokelisia marginata*), in the 24 April and 5 May samples. Both of these insects are found throughout the marsh but are not randomly distributed at any one time. A square meter quadrat may contain a high density of

TABLE 32				
DENSITY, DRY BIOMASS AND ENERGY CONTENT OF INSECTS AND SPIDERS AS DETERMINED BY THE ONE SQUARE METER QUADRAT BAG HARVEST METHOD				
Date	Marsh Type	Ind/m ²	Mgm/m ²	Gcal/m ²
4 March	Levee	591	506	2270*
24 April	Levee	2086	855	4197**
5 May	Streamside	300	316	1120**
26 May	Levee	35	19	225
5 June	Streamside	268	204	959*
14 June	Levee	225	189	987*
25 June	Streamside	164	102	507
3 July	Levee	89	43	360
18 July	Streamside	171	87	470
4 August	Levee	124	109	527
	Mean	405	246	1162
	S.D.	1930	260	1218
	C.V.	476	107	104

* High density of marsh ants (*Crematogaster clara*) in quadrat

** High density of marsh fulgorids (*Prokelisia marginata*) in quadrat

Prokelisia or *Crematogaster* while another quadrat nearby may be almost devoid of these insects. High local density of insects in tall grass where wrens spend most of their time is important in enabling the wrens to catch their prey with relatively little effort.

From these preliminary data I estimated that the standing crop of potential wren food per square meter probably averages about 500 insects and spiders (range: 35-2000 individuals/m²), which have a mean dry biomass of approximately 300 mgm (range: 20-900 mgm/m²), and a mean energy content of 1500 gcal (range: 200-4200 gcal/m²).

STOMACH CONTENTS

The volume of the contents of 184 stomachs as measured by volume displacement in a graduated cylinder ranged from 0.075 to 0.350 ml per stomach with a mean of 0.150 ml. The frequency distribution of food volumes is shown in Table 33. Wet weights in milligrams of 21 fresh stomachs are shown in Table 34. As shown in Table 33 only 16% of the stomachs contained less than 0.100 or more than 0.250 ml of food. Assuming the specific gravity of stomach contents to be 1, the wet weight of the average standing stock of food in the stomach would be 150 mgm. The average of the 21 wet stomachs that were weighed (Table 34) was somewhat higher, 186 mgm; however, the majority of these stomachs contained more than 0.150 ml of food. Thus

TABLE 33		
FREQUENCY OF WREN STOMACHS CONTAINING DIFFERENT VOLUMES (WET) OF FOOD (N = 184)		
Volumes (ml)	Number of Stomachs	Frequency (percent)
Less than 0.075	0	0
0.075-0.100	15	8
0.100-0.150	80	43
0.150-0.200	28	15
0.200-0.250	47	36
0.250-0.300	5	3
0.300-0.350	7	4
0.350-0.400	2	1

TABLE 34					
WET WEIGHT IN MILLIGRAMS OF CONTENTS OF 21 WREN STOMACHS					
Volume Interval (ml)	0.075-0.100	0.100-0.150	0.150-0.200	0.200-0.250	0.250-0.300
	100	130	166	210	310
		150	190	271	290
		150	184	214	297
		120	222		
		126	174		
		149	190		
		110			
		147			
Class Mean:	100	135	188	232	299
Mean of all weights: 186 mgms					

the mean wet weight of stomach contents is probably closer to 150 mg.

Percent frequency of occurrence and percent total volume of the major groups of food items found in 195 stomachs of marsh wrens collected throughout the year are presented in Table 35.

Food items eaten during the breeding season, April through August, are compared with those eaten in the winter season, September through March, in Figure 21 and Tables 36 and 37. There was a pronounced increase in frequency and volume of the marsh fulgorid (*Prokelisia marginata*) from 47% (12% volume) during the summer to 87% (40% volume) in winter, paralleling the population growth of this homopteran, which reaches its peak of population density during the cooler months (Smalley, 1959, and personal observations).

TABLE 35			
MEAN PERCENT FREQUENCY OF OCCURRENCE AND PERCENT TOTAL VOLUME OF FOOD ITEMS IN 195 WREN STOMACHS COLLECTED THROUGHOUT THE YEAR			
Food Item	Number of Stomachs	Frequency (percent)	Percent Total Volume*
Total Hymenoptera	157	80.5	15.4
Formicidae	89	45.7	9.1
Ichneumonidae	10	5.1	0.2
Braconidae	42	21.6	2.7
Chalcididae	29	14.9	1.1
Others	95	48.7	2.5
Total Homoptera	133	68.2	23.7
Fulgoridae	124	63.6	23.0
Total Coleoptera	133	68.2	12.0
Curculionidae	69	35.4	5.4
Anthribidae	8	4.1	0.4
Cleridae	42	21.6	2.4
Melyridae	14	7.2	1.1
Mordellidae	28	14.4	1.4
Others	22	11.3	0.4
Larvae	18	9.2	1.1
Total Diptera	90	46.2	8.4
Ephydriidae	27	13.8	3.6
Otitidae	26	13.3	1.2
Dolichopodidae	14	7.2	0.7
Others	38	19.5	2.8
Larvae	15	7.7	1.3
Total Hemiptera	81	41.6	7.2
(<i>Ischnodemus badius</i>)			
Total Lepidoptera	47	24.1	9.9
Larvae & Eggs	37	19.0	7.4
Total Orthoptera	14	7.2	3.8
(<i>Orchelimum fidicinum</i>)			
Total Spiders	131	67.2	11.6
<i>Grammonota georgiana</i>	63	32.3	2.5
<i>Clubiona littoralis</i>	19	9.8	2.0
<i>Marpissa</i> spp.	31	15.9	3.5
<i>Dictyna altamira</i>	17	8.7	0.8
Other Araneida	52	26.68	3.2
Other Arthropods	31	15.9	2.0
Crabs	17	8.7	0.5
Amphipods	8	4.1	0.8
Barnacles	5	2.6	0.6
Pseudoscorpions	4	2.0	0.03

TABLE 35 (Continued)

Food Item	Number of Stomachs	Frequency (percent)	Percent Total Volume*
Total Molluses	47	24.1	3.6
<i>Littorina irrorata</i>	23	11.8	2.0
<i>Melampus bidentatus</i>	27	13.8	1.0
<i>Littoridinops</i> sp.	15	7.7	0.7
Undetermined animal matter (insects)	50	25.6	4.0
Total Insect Eggs	18	9.23	2.0

* Total volume = 28.38 ml.

The most frequent food items during the breeding season were spiders, found in 78% of the stomachs analyzed. However, spiders comprised only 15% of the volume of stomach contents. This was because of the small size of the most frequently eaten species, the linyphiid, *Grammonota georgiana*, and the dictynid, *Dictyna altamira*. Both species are only one to three millimeters in size and weigh approximately 0.1 mg.

Hymenoptera, chiefly ants (Formicidae) and small parasitic wasps (Braconidae, Chalcididae, Ichneumonidae, and Scelionidae) were found in 76% of the stomachs. The Formicidae, chiefly the marsh ant (*Crematogaster clara*), composed over 50% of hymenopteran food items.

The hemipteran, *Ischnodemus badius*, doubled in importance as a food item in winter (28% frequency-5% volume in summer, compared with 60% frequency-10% volume in winter).

The Diptera remained at about the same levels of frequency and volume throughout the year, although twice as many larvae (mainly Ephydriidae) were eaten in winter as in summer. This is not unexpected because the larvae of many species of the Ephydriidae and other salt marsh diptera feed on dead and decaying vegetation. Large amounts of dead *Spartina* are present in the marsh in winter.

Coleoptera occurred in more stomachs in winter (82%) than in summer (58%) but remained relatively constant in volume (12%) throughout the year. Certain species of beetles occurred in more stomachs at one season than at another. The marsh curculionid (possibly *Lissorhopturus* sp.) was found in 51% of the stomachs in winter, but only 24% during the summer. Conversely, the clerid, *Isohydnocera tabida*, was found in 30% of the summer wrens, but only 10% of the winter population.

The long-horned marsh grasshopper (*Orchelimum fidicinum*), which reaches 40-50 mm. in size, occurs in relatively few adult

TABLE 36			
MEAN PERCENT FREQUENCY OF OCCURRENCE AND PERCENT TOTAL VOLUME OF FOOD ITEMS IN 113 WREN STOMACHS, APRIL-AUGUST			
Food Item	Number of Stomachs	Frequency (percent)	Percent Total Volume*
Total Hymenoptera	86	76.1	17.3
Formicidae	50	44.2	10.2
Ichneumonidae	7	6.2	0.3
Braconidae	29	25.7	3.7
Chalcididae	23	20.4	1.6
Others	46	40.7	2.5
Total Coleoptera	66	58.4	11.6
Curculionidae	27	23.9	3.6
Anthribidae	7	6.2	0.6
Cleridae	34	30.1	3.5
Melyridae	9	8.0	1.6
Mordellidae	17	15.0	1.6
Others	6	5.3	0.2
Larvae	14	12.4	1.4
Total Homoptera	61	54.0	13.0
Fulgoridae	53	46.9	11.9
(<i>Prokelisia marginata</i>)			
Total Diptera	54	47.8	8.9
Ephydriidae	9	8.0	2.8
Otitidae	18	15.9	1.3
Dolichopodidae	11	9.7	0.7
Others	25	22.1	4.0
Larvae	5	4.4	0.3
Total Lepidoptera	35	31.0	14.6
Larvae & Eggs	25	22.1	10.4
Total Hemiptera	32	28.3	5.4
(<i>Ischnodemus badius</i>)			
Total Orthoptera	11	9.7	5.6
(<i>Orchelimum fidicinum</i>)			
Total Spiders	88	77.9	15.1
<i>Grammonota georgiana</i>	35	31.0	1.9
<i>Marpissa</i> spp.	26	23.0	5.1
<i>Clubiona littoralis</i>	16	14.2	3.2
<i>Dictyna altamira</i>	15	13.3	1.2
Other Araneida	33	29.2	4.0
Other Arthropods	17	15.0	1.8
Crabs	10	8.8	0.5
Amphipods	6	5.3	1.2

TABLE 36 (*Continued*)

Food Item	Number of Stomachs	Frequency (percent)	Percent Total Volume*
Other Arthropods (<i>Continued</i>)			
Barnacle	4	3.5	1.0
Pseudoscorpion	4	3.5	0.05
Total Molluscs	20	17.7	3.5
<i>Littorina irrorata</i>	10	8.8	2.4
<i>Melampus bidentatus</i>	10	8.8	1.0
<i>Littoridinops</i> sp.	3	2.7	0.1
Undetermined animal material (insects)	30	26.6	4.5
Total Insect Eggs	11	9.7	0.6

* Total volume = 17.15 ml.

stomachs, usually represented then by eggs, but is an important part of the diet of nestlings and fledglings. Seven of the ten wren stomachs in which grasshopper nymphs or adults were found during the breeding season were from young birds.

Moths and moth larvae, which are also relatively large food items, were found in more nestling than adult stomachs. The frequency of Lepidoptera in adult and nestling stomachs during the breeding season was twice the frequency in winter stomachs while percent volume increased fivefold.

Other arthropods including barnacles, amphipods, crabs, and pseudoscorpions occurred in approximately 16% of the stomachs. Although crabs, especially *Uca* sp., and *Sesarma* sp., are very abundant in the bed of the marsh, they occurred in only 9% of the stomachs. This is not surprising, since I saw no wrens feeding on the marsh substratum.

Molluscs were found in 24% of the wrens, with almost twice as many stomachs containing snails in winter (33%) as in summer (18%). Judging from the condition of some of the shells, the snails may have been dead before being eaten by the wrens. Molluscs are probably utilized for grit since sand grains were rarely found in wren stomachs.

Twenty of the 195 stomachs analyzed were from nestlings and fledglings. As mentioned previously, the majority of these 20 stomachs contained remains of relatively large insects that rarely appeared in adult stomachs. These include the marsh grasshopper (*Orchelimum fidicinum*), the horsefly (*Tabanus nigrovittatus*), various adult moths, moth larvae, and lycosid spiders.

Table 38 presents a comparison of sizes of items found in six nestling stomachs with those found in six adult stomachs collected at relatively

TABLE 37			
MEAN PERCENT FREQUENCY OF OCCURRENCE AND PERCENT TOTAL VOLUME OF FOOD ITEMS IN 82 WREN STOMACHS, SEPTEMBER-MARCH			
Food Item	Number of Stomachs	Frequency (percent)	Percent Total Volume*
Total Homoptera	72	87.8	40.1
Fulgoridae	71	26.6	39.8
(<i>Prokelisia marginata</i>)			
Total Hymenoptera	71	86.6	12.4
Formicidae	39	47.6	7.4
Ichneumonidae	3	3.7	0.2
Braconidae	13	15.9	1.2
Chalcididae	6	7.3	0.3
Others	49	59.8	2.6
Total Coleoptera	67	81.7	12.6
Curculionidae	42	51.2	8.2
Anthribidae	1	1.2	0.1
Cleridae	8	9.8	8.9
Melyridae	3	3.7	0.1
Mordellidae	11	13.4	1.2
Others	16	19.5	0.8
Larvae	4	4.9	0.5
Total Hemiptera	49	59.8	10.0
(<i>Ischnodemus badius</i>)			
Total Diptera	36	43.9	7.7
Ephyridae	18	22.0	4.8
Otitidae	8	9.8	1.0
Dolichopodidae	3	3.7	0.6
Others	13	15.9	1.0
Diptera larvae	10	12.2	2.8
Total Lepidoptera	12	14.6	2.9
(only larvae and eggs)			
Total Orthoptera	3	3.7	0.8
Total Spiders	43	52.5	6.2
<i>Marpissa</i> spp.	5	6.1	1.0
<i>Clubiona littoralis</i>	3	3.7	0.1
<i>Grammonota georgiana</i>	28	34.2	3.3
<i>Dictyna altamira</i>	2	2.4	0.01
Other Spiders	19	23.2	1.9
Other Arthropods	10	12.2	0.9
Barnacle	1	1.2	0.01
Amphipods	2	2.4	0.2

TABLE 37 (Continued)

Food Item	Number of Stomachs	Frequency (percent)	Percent Total Volume*
Other Arthropods (Continued)			
Crabs	7	8.5	0.6
Pseudoscorpion	0	0	0
Total Molluscs	27	32.9	4.0
<i>Littorina irrorata</i>	13	15.9	1.2
<i>Meampus bidentatus</i>	17	20.7	1.1
<i>Littoridinops</i> sp.	12	14.6	1.6
Undetermined animal material (insects, larvae, and eggs)	20	24.4	3.3
Total Insect Eggs	7	8.5	0.4

* Total volume = 11.22 ml.

TABLE 38

COMPARISON OF SIZE OF FOOD ITEMS IN STOMACHS OF SIX NESTLINGS
AND SIX ADULTS COLLECTED AT SAME TIME AND PLACE

Food Item	Number of stomachs		Mean dry weight of food item (mgm) *
	Nestlings (6)	Adults (6)	
<i>Orchelimum fidicinum</i>	6	0	70.0
<i>Tabanus nigrovittatus</i>	2	0	60.0
Lycosidae	3	0	14.0
Lepidoptera larvae	1	2	12.4
<i>Marpissa bina</i>	4	1	10.0
<i>Clubiona littoralis</i>	3	0	5.4
<i>Poecilochroa</i> sp.	1	0	5.4
Sarcophagidae	1	0	5.2
Undet. spiders	0	1	2.0
<i>Ischnodemus badius</i>	0	2	1.3
<i>Isohydnocera tabida</i>	0	2	1.2
<i>Chelonus</i> sp.	0	1	1.0
Anthribidae	0	1	0.8
Formicidae	1	3	0.5
<i>Prokelisia marginata</i>	2	5	0.5
Small wasps	1	5	0.4
<i>Grammonota georgiana</i>	2	5	0.2
Small molluscs	3	1	0.1

* Listed in order of decreasing size.

the same time and from the same area. Most of the food items of adults were less than 10 mm in length or 5 mg in weight (dry), and very few were over 15 mm in length or 12 mg in weight. On the other hand food items in nestling stomachs ranged up to 30 mm in length and 70 mg in weight.

DISCUSSION

RESPIRATORY ENERGY FLOW ESTIMATES

Experiments comparing the food consumption and the oxygen consumption methods are summarized in Table 39. Only those values

TABLE 39
COMPARISON OF RESPIRATORY ENERGY FLOW ESTIMATES OF WRENS BASED ON
O₂ AND FOOD CONSUMPTION MEASUREMENTS

	Food Consumption	O ₂ Consumption	
		Inactive	Active
No. Individuals	10	10	10
No. Measurements	124	30	28
Duration Measurements	7 days	3-4 hrs	3-4 hrs
Gcal/gm $\times$ hr $\pm$ S.E.	36.5 $\pm$ 0.2	23.3 $\pm$ 0.7*	34.7 $\pm$ 1.0*
S.D.	2.3	3.6	5.3
C.V.	6.4	15.7	15.4

* ml O₂ $\times$ 4.93 $\times$ 10⁻³.

within the thermoneutral zone (23°-35°C) were considered for this comparison. Values of oxygen consumption for active and inactive individuals are listed separately. Many of the inactive wrens were at basal or near basal level, while the active wrens were either free to move about in the respirometer, or, if restrained in boxes, were fairly active while confined.

Mean respiratory energy at near basal conditions was 23.3 $\pm$ 0.7 gcal/gm $\times$ hr (5.81 kcal/bird $\times$ day) compared with the value of 36.6 $\pm$ 0.2 gcal/gm $\times$ hr (8.8 kcal/bird $\times$ day) obtained in the feeding experiments. The mean value for active wrens in the respirometer was 34.7 $\pm$ 1.0 gcal/gm $\times$ hr (8.21 kcal/bird $\times$ day), which is similar to the mean obtained during the feeding experiments. Respiratory energy values of the near basal wrens were approximately 35% lower than values determined by feeding experiments.

Odum, Connell, and Davenport (1962) found that the respiratory rate of old-field mice (*Peromyscus polionotus*) as determined by food consumption was approximately 38% higher than that determined by measuring oxygen consumption. For insects they found that food consumption respiratory rates were double those obtained in a respirometer.

More recently W. Grodzinski (in *litt.*-E. P. Odum) has found that values of existence energy of small mammals as determined by oxygen consumption is similar to values determined by feeding experiments when the respirometer is sufficiently large to contain suitable nesting material, food, and water, and the oxygen consumption is determined over a longer period (12-24 hours or more).

From the data presented here I concluded that it is possible to obtain values for existence energy of small, active birds in an oxygen respirometer similar to that obtained by long-term food intake measurements so long as the birds are not in a basal condition and are permitted to move freely in the chamber.

On the basis of work of Brody (1945) and others (see Odum, 1960), Odum et al. (1962) estimated that energy needed by vertebrates to survive in the field is about double that needed in confinement. On the other hand, Uramoto (1961), who also reviewed the work of several authors, concluded that wild birds require only 30-50% more energy than do captive birds. Undoubtedly the natural behavior and activity of a species determines how much above the confinement existence energy the natural existence energy requirements will be.

LeFebvre (1964) found that energy expenditure in flight (sustained strenuous work) is approximately eight times the energy expenditure of a resting domestic pigeon. The Savannah Sparrows studied by Connell (1959) are also strong fliers. They range over a wide area in winter. Therefore, confinement in cages reduces their activity considerably. Although Connell did not actually determine energy requirements of the Savannah Sparrow in the field, it was estimated that this expenditure would be double that needed in captivity (Odum, et al., 1962). In contrast, Long-billed Marsh Wrens are relatively slow, short distance flyers, and much of their movement consists of hopping from stem to stem in the dense stands of marsh grass. During the breeding season movement of *griseus* is limited primarily to a small territory approximately 100 m² in size. In captivity marsh wrens are extremely restless and are in constant motion most of the day. Even when wrens are confined in a small box considerable movement may be observed. For these reasons I estimate that the additional respiratory energy required by *griseus* is probably not more than 30% greater than that needed when confined in small cages at about 1/50 of a cubic meter in volume.

POPULATION ECOLOGY

Territoriality. In the marsh wren population where courtship, mating, nesting, and food seeking occur within a defined area (Nice's, 1941, Type A territory), territory size is the basis for determining

population densities in the utilized areas. For this reason I placed much emphasis in this study on territoriality.

T. p. griseus frequently establishes territorial boundaries along drainage channels, as shown in Fig. 16. These channels, which vary in depth, dissect the levees at irregular intervals. Where the channels are shallow and overgrown with grass they may or may not be used to delimit territory. In such cases the boundaries are defined by the singing male and may vary a meter or so in one direction or the other. Territory size appears to be influenced by the physiography of the habitat. In areas where tall *Spartina* is in narrow strips (1-3 meters wide), or is dissected by regions of slumping levees with shorter grass, a territory may be extensive.

In 1959 I made an analysis of differences between territories located in dissected habitats and territories in continuous habitats. The mean maximum area of territories 1-6 and 18, in the dissected habitat of Area 4 (Fig. 16) was $120 \pm 35 \text{ m}^2$. Territories 7-17 were located in habitat consisting of a broad, continuous band of dense grass and comprised a mean area of $100 \pm 14 \text{ m}^2$. The inhabitable tall *Spartina* or utilized territory area was actually less in the dissected habitats than in the continuous habitat. Mean utilized territory area for territories 18, and 1-6 was only $61 \pm 18 \text{ m}^2$. The mean utilized territory size of all the territories in Area 4 in 1959 was $82 \pm 12 \text{ m}^2$ (Table 4), which is similar to the mean utilized territory size in Area 2 in 1959 ($85 \pm 9 \text{ m}^2$). The mean maximum territory size for all the territories in Area 4 was $107 \pm 14 \text{ m}^2$. Because all of the territory areas in Area 2 contained inhabitable tall grass, no distinction is made between maximum and utilized area.

The significant point here is that the amount of tall grass present in a territory is not as variable as the amount of land. This is to be expected since it is in the tall grass habitat that the wren conducts all of its breeding activities. Therefore it is the acreage of tall grass, and not the land surface area, that plays the important part in determining the size of the territory.

A difference in territory sizes in Area 2 between 1958 and 1959 was noted earlier (Table 5). An analysis of variance indicated that Area 2 in 1958 differed significantly in mean territory size from Area 1 in 1958 and Areas 2 and 4 in 1959. The larger territories in 1958 appear to be due to factors concerned with the weather conditions of the previous winter.

Differences in the growth rate of *Spartina* and survival rates of overwintering insect populations due to the dissimilar weather conditions at the beginning of the two breeding seasons may have played an important effect upon territory size. The severe winter of 1957-1958 retarded winter growth of the *Spartina* and probably killed some of the wren's insect food. Since the grass was shorter (0.5 m high)

when breeding was started in 1958 and the insect population possibly reduced, more area would then be needed in each territory. In 1959 (and in 1960-1961), the marsh grass was already a meter or so high when territories were established. Because the mild winter had a less adverse effect upon the overwintering and early spring insect populations, more food may have been readily available in a smaller area. Hinde (1956) concluded that it is possible that the territorial behavior in species that restrict feeding to their territories helps to insure an adequate supply of food for the young.

Another possibility is that a lower population density may have resulted in a larger territory size in 1958. Kendeigh (1941) reported that the size of a male House Wren's territory appears to be compressible down to a minimum size with increasing number of birds present. Such a trend is also reported by Kluiyver and Tinbergen (1953) and Hinde (1956). Kendeigh (op. cit.) adds that the "size of the territory is flexible and, within limits, varies inversely with the size of the population present." He points out that individuality inherent in each bird prevents one from making any hard and fast rule concerning territory preference and size. The variability in size of *griseus* territories certainly suggests that territory size is flexible in this race and may be related to the amount of desirable grass habitat available and the physical ability of a male to defend a larger area.

Ivan R. Tomkins (1959, in *litt.*) observed near Savannah, Ga., what appeared to be marsh wren concentrations caused by dredging operations, which resulted in drying up of a portion of the marsh. He theorized "that there was homing of the normal population and consequent crowding."

From my observations I believe that there were fewer breeding pairs of wrens in the marsh as a whole in 1958 than there were in subsequent years, but I have no quantitative data to substantiate this opinion, since the watershed census was not begun until 1959.

A factor of some importance influencing territory size and population density is the preference of *griseus* for colonial living. Rarely is an isolated wren territory found. Usually there will be several other territories nearby. There are several areas in the Duplin River marshes that appear to offer suitable wren habitat, but they are not occupied every year. The requirements for desirable habitat appear to include a high, well developed levee, covered with a dense stand of *Spartina* at least 1.5 m tall and from 2-5 or more meters in width. Early in the season, such areas contain relatively dense stands of tall dead *Spartina* left from the previous year. In April, 1958, several males established territories in Study Area 3. In mid-May the wrens started moving from the area, and by 1 June no wrens could be found. In June, 1959, several active territories were being maintained there.

The proximity of other wrens seems to be an important requirement in the selection of nesting territories.

Destruction of wren habitats by winter storms, especially in those areas located on the channel cutting side of the streams, determines largely the availability and use of habitat in those areas the following season. Destruction of habitat occurs in two ways: (1) In the winter and early spring huge rafts of dead *Spartina* float out to sea on each ebb tide. During periods of spring tides many of these rafts are deposited on the streamside and levee marsh. If these remain for a period of time, the growing *Spartina* beneath is flattened and shaded and consequently dies. When the stranded rafts of grass are removed by later tides, a bare patch of mud is exposed. Depending upon the extent of the denuded area it may take several seasons for the *Spartina* to repopulate the area. (2) The second type of habitat destruction occurs during periods of heavy rainfall. This occurs primarily in the autumn when as much as ten inches of rain may fall in September or October if a hurricane passes along the coast. Under the influence of heavy rains the banks of the creeks cave in. This slumping is accentuated during periods of very low tides and occurs most frequently on the channel side of a stream.

Mortality. Mortality plays a leading role in determining population densities. While it is relatively simple to ascertain egg and nestling mortality in a breeding population, the gradual dispersal of the fledglings away from their nest territories, the denseness of the habitat, and the retiring nature of nonbreeding birds often prevent actual determination of fledgling and adult mortality. Deevey (1947) concluded that "all natural populations of birds so far investigated in any detail appear to be alike in suffering a constant annual risk of death from early adult life to the end of the life span." He found that this mortality was about 32% per year. Several other authors (Kendeigh, 1934; Nice, 1937; Kluiyver, 1951; Johnston, 1956; and Mayhew, 1958) make estimates ranging up to about 50% per year. Since *griseus* is, by and large, a year round resident, its annual adult mortality rate should be lower than the rate for similar sized migratory birds. Deevey's figure of 32%, then, probably represents a maximum annual adult mortality.

By referring to the watershed census figures for 1959 and 1960 (Table 13) and assuming no immigration from other areas in 1960, it should be possible to estimate the mortality of the 1959 fledglings. Of the 940 adults in the Duplin River watershed in 1959, a maximum of around 300 (32%) probably died over the winter, and 640 survived to the next breeding season. Since each pair of adults in the 1959 study areas fledged an average of 2.15 young, a total of 980 young was fledged. In order to maintain a stable breeding population there should be an annual recruitment of young wrens equal to the number

of adults lost. The census estimates made in 1960 indicated substantially the same population density in the Duplin River watershed as in 1959. Therefore a minimum of 300 fledglings or 30.6% of those produced in 1959 survived the first year of life. Conversely, this would indicate that fledgling mortality was around 70%. It should be pointed out that immigration into the watershed is thought to have occurred in the 1961 and 1962 breeding seasons. Thus immigration, or emigration, could have occurred in the 1960 season. If such was the case, then the above estimates will be somewhat inaccurate.

The most critical period in the life of altricial birds is during the egg and nestling stages. The evolution of rapid nestling growth and subsequently shortened nest life is undoubtedly an adaptational response on the part of birds to insure nesting success. Predation is usually the chief cause of mortality during the nestling stage. Raccoons (*Procyon lotor*), Rice Rats (*Oryzomys palustris*), and mink (*Mustella vison*), particularly the first two, were the chief predators of *griseus*. In 1958 a little more than half of the predation was caused by raccoons (and possibly mink), while rat predation amounted to about 37%. The extremely high mortality of eggs and nestlings from Rice Rat predation in 1959 and 1960 (Tables 8 and 9) was the result of a large increase or "bloom" in the *Oryzomys* population. Wayne (Sprunt and Chamberlain, 1949) mentioned predation of young wrens by "mice which live in the marsh." Since most of the rats observed in the Sapelo marshes were small, it is possible that Wayne was referring to *Oryzomys*. In fact Dr. Chamberlain informs me that Wayne's original published statement appeared in his *Birds of South Carolina* published in 1910. Bent (1948) cites this same statement: ". . . and a mouse (*Hesperomys*-now *Peromyscus leucopus*), which lives in the marsh and builds a nest similar to that of the wren, commonly takes possession of the nest and often eats the eggs as well as the young." Chamberlain regards Wayne's indictment of *Peromyscus* as an error and believes that *Oryzomys* is the animal Wayne actually saw.

Nicholson and Wheeler (Wheeler, 1931) mentioned predation upon *T. p. marianae* in Alabama marshes by "rats and mice which are abundant in all salt marshes," but they did not give scientific or common names.

Predation by Rice Rats affected nesting success more toward the end of the season in 1959 than at the beginning. This is shown by Fig. 8 where the numerous small peaks in 1959 indicate repeated renesting attempts and repeated failures. Since an adult female rat may have up to three litters of three to six young each during the breeding season (Conaway, 1954, and personal observations), an increase in rat population would cause an increase in predation of nests by rats as the season progressed.

In 1960 rat predation seemed to be amplified by the frequent high

spring tides that occurred during the breeding season. Many of the wren nests that escaped high water were immediately occupied by rats that had been forced out of their own inundated nests located at lower levels in the marsh. Thus the high tides of 1960 caused greater rat predation than might have occurred normally. As a consequence no nestings were successful until August and only 16 new wrens were fledged in the study areas. Because I saw fledglings outside the study areas by mid-July, I thought that mortality was perhaps not so severe in other areas in 1960.

The major portion of the diet of Rice Rats consists of crabs and insect larvae (Sharp, 1962); hence wrens play only an insignificant role as a food source. However, the wrens are highly vulnerable during the nesting season when rats utilize wren nests for sleeping quarters during the day and for rearing their young.

In 1961 predation by raccoons exceeded that by Rice Rats although observations indicated that the rat population was still at a high peak. An indication that the raccoons (possibly mink also) were actively searching for wrens or rats was my observation that in several territories every nest was knocked down and torn open. I had not observed such complete destruction within a territory during the previous three years. Perhaps the greatly increased numbers of rats in the marsh had attracted the attention of the raccoons and mink, which normally feed on the numerous marsh invertebrates (crabs, mussels, and shrimp).

It is possible that the percentage of eggs lost by drowning throughout the marsh was higher than indicated by the value obtained in the study areas in 1959. During the extremely high tide on 22 June I noted that half of the territories in Area 4 and most of the territories in Area 2 were on higher levees than many of the other territories along Duplin River and Barn Creek. On the other hand, there are other circumstances besides the levee elevation which contributed to a low drowning mortality. For instance, in 1958 young of the first brood were fledged by 31 May, when the only drowning tide of the season occurred. In 1959 the drowning tides occurred two weeks earlier, but since nesting was started earlier, the young of successful first broods were fledged before the highest tides covered the nests.

The early growth of *Spartina* in 1959 allowed nests to be built higher in the grass, thus escaping the May tides. In June, with continued growth, newer nests were built still higher and also were above high water during the June tides. Finally, the low drowning mortality may also be due to the increased rat predation. As a result of nest losses from rats many second brood nest attempts were unsuccessful so that at the time of the June spring tide, there were not as many nests with eggs and young in the marsh as there might have been if rat predation had been less.

Spring tides when unaccompanied by easterly winds rarely cover wren nests. In 1961 no eggs or young were drowned. However, in 1960, when strong easterly winds coincided with the spring highs from April to July, wren mortality increased considerably (21%).

Johnston (1956) found that flooding accounted, on the average, for the destruction of 11.8% (range 2.8-24%) of all salt marsh Song Sparrow eggs laid. He hypothesized "that selection has fitted the song sparrows of the marsh to early breeding so that . . . the birds breed before the high run of high tides and thus escape a chief cause of mortality in the young age classes." There is no evidence that breeding by *T. p. griseus* is in any way attuned to avoid high tides. The marsh wren is, however, pre-adapted to the tidal salt marsh habitat of the southeastern coast because it has a long breeding season.

Nesting success. Many factors affect nesting success, and it is only after the study of a number of breeding seasons that an "average" or "normal" percentage can be determined. Nice (1937), Peterson and Young (1950) and Evans (unpublished data) indicate average nesting success percentages of between 40 and 50% as normal for open nesting passerines in temperate North America. In hole nesting species the percentage averages somewhere between 60 and 80% (Allen and Nice, 1952; Kendeigh, 1942; Skutch, 1953). The average nesting success of the marsh wren, in view of the unique closed nest constructed, should be perhaps somewhere between these two averages.

Whether or not the 42% nesting success for *griseus* in 1958 (Table 10) represents an average or normal season remains to be seen. At the present time I believe that this value reflects a better than average season. This premise is based upon two facts: (1) there was only one drowning tide in 1958, whereas it is possible to have them each month during the breeding season, as occurred in 1960. (2) Predation was relatively low in 1958 as compared with 1959-1961.

The low percentage of success in 1959-1961 does not necessarily mean that all of the wren populations throughout the Georgia coastal marshes experienced the same conditions causing low nesting success. It seems unlikely that high Rice Rat densities occurred everywhere. Immigration of wrens into an area of low fledgling production from one with high nesting success is very likely in a habitat as vast and extensive as the southeastern Atlantic coast tidal marshes.

POPULATION DENSITY

I have considered three different types of estimates of density (Table 13) in this study because each type contributes information not revealed by the others. Two of these—crude density and ecological or specific density—have been used by other researchers. The crude density (0.5 pr/ha or 0.2 pr/acre) is a rather unrealistic estimate

because the wrens are not found throughout the marsh, but the estimate does give an indication of the low numbers of wrens actually found in the total marsh.

The ecological density of 45-56 pr/ha (18-23 pr/acre) represents the number of birds in relation to the available wren habitat, i.e., tall streamside and levee *Spartina* marsh. This is a very high density in comparison with other habitats. The highest population densities, which include *all* breeding species, reported in the Audubon bird censuses (Udvardy, 1957) such as those found in fertile mixed bottom-land and flood plain forests, are rarely greater than 10 pr/acre. Thus the density of the single species population of wrens is greater in the tall grass habitat than the density of mixed species populations is in most land habitats.

The ecological density does not present the complete picture of wren densities in the salt marsh, because the wrens do not utilize all of the habitat. Therefore a third density estimate—the occupied or utilized area density, based upon Odum and Kuenzler's (1955) utilized territory concept—was determined and found to be approximately 98-109 pr/ha (41-45 pr/acre). It should be emphasized that this extremely high density does not appear so spectacular when one considers that tall grass marsh is among the most productive natural communities. Thus high wren density may be reflecting high primary productivity with consequent high insect production. Udvardy (1957) also considers high bird density in marshes as a direct result of higher organic productivity of marshes in general. This high productivity enables species that adapt to a marsh habitat to maintain small territories and thus reach locally high densities.

FACTORS LIMITING POPULATION DENSITY

The number of wrens in the Duplin River watershed at the beginning of each season was similar in each of four years, 1959-1962 (Tables 13 and 22). Only in 1962 was there a decided increase (approximately 100 pairs) in numbers. Nevertheless, in terms of potential wren habitat, the ecological density was increased by only ten pairs per hectare (4 pairs per acre), while the occupied density remained unchanged.

The standing crop of adult wrens in the intensive study areas was also similar each year regardless of the fledgling production (nesting success) of the previous season (Tables 11 and 22). Perhaps the vast expanse of coastal *Spartina* marsh, which extends from the Carolina coast to northern Florida, acts as a huge reservoir or buffer system for the animal populations living in it. Low reproductive success in one part of the marsh may be balanced by higher production elsewhere. No noticeable changes in population size over a five

year period in any of the important macrofauna of the salt marsh were detected by Teal (1962). He observed that the salt marsh ecosystem exhibits considerable stability.

Odum et al. (1962) point out that "The most debated questions in population ecology theory at the present time revolve around the question of whether the size of natural populations of this or that species is limited by available energy or whether the density is kept below the food carrying capacity by physical factors (weather, etc.), intra- or inter-specific strife (fighting, territoriality, etc.), predation, or other limiting factors not directly limited to energy flow." If energy is limiting, "then intra- and inter-specific competition for food should act in a density-dependent manner and provide the major mechanism for population control." If other limiting factors control population size, "then density-dependent competition may be of less importance."

An analysis of the factors possibly limiting the wren population follows:

(1) *Food*

T. p. griseus is a predator that feeds upon animals at three different trophic levels—herbivores, predators, and detritus feeders (Fig. 20 and Tables 35-37). Detritus feeders are animals that feed on particulate organic material originating from dead bodies of organisms (Odum and De la Cruz, 1963). However, I am also including in this category those organisms that feed on dead, decaying *Spartina* (various Diptera larvae). According to Hairston, Smith and Slobodkin (1960) predator populations are often limited by food. But a predator that occupies a broad food niche is not helplessly dependent upon any single prey population, and in this sense food might not be a limiting factor, especially if the predator itself is subjected to predation.

The mean estimated daily energy intake of a marsh wren is approximately 12 Kcal/day (Table 24). Therefore a wren must obtain approximately $120 \text{ gcal/m}^2 \times \text{day}$ for body maintenance from the average territory of 100 m^2 . According to the preliminary estimates of insect and spider densities in wren habitats (Table 32) this represents about 8% of the estimated mean standing crop of food. However, the wren conducts all of its activities within this 100 m^2 during the breeding season of approximately 140 days. Table 40 presents the estimated energy requirements of a hypothetical "typical" marsh wren family during this period of time. On the basis of life history data it is estimated that an "average" pair of wrens produces 9 eggs, three of which hatch, and two of which fledge. From these calculations one can see that average seasonal energy intake is approximately $280 \text{ gcal/m}^2 \times \text{day}$, or approximately 19% of the estimated mean standing crop of insects and spiders.

TABLE 40							
ESTIMATED ENERGY REQUIREMENTS OF A HYPOTHETICAL "TYPICAL" WREN FAMILY DURING THE BREEDING SEASON IN AN AVERAGE SIZE TERRITORY OF 100M ² *							
(1) Respiration	No. Ind.	Kcal/ bird × day			No. Days	Energy (Kcal.)	
Adults	2	×	9.0	×	140	=	2520
Nestling (assumed to survive only 7 days)	1	×	2.7	×	7	=	19
Fledglings	2	(see below)			25	=	242
(As nestlings)							
Age 1-5	2	×	0.5	×	5	= (5)	
5-10	2	×	2.7	×	5	= (27)	
10-15	2	×	5	×	5	= (50)	
(As fledglings)	2	×	8	×	10	= (160)	
							(242)
						Subtotal:	2781
(2) Production	No. Ind.	Dry Weight (gm/ind.)		Kcal/gm			
Eggs	9	×	.17	×	6.74	=	10
Nestling	1	×	1.5	×	6.13	=	9
Fledglings	2	×	2.8	×	6.71	=	38
						Subtotal:	57
	Total Seasonal Energy Flow						2838
	Energy Flow/100m ² × day						20
	Energy Flow/m ² × day						.20
(Assimilation Efficiency = 70%)	Gross Energy Intake/m ² × day						.28
(5.62 Kcal/gm × insects)	Milligrams insects/m ² × day = 50 mgm						

* 2 adults, 9 eggs, 3 nestlings, 2 fledglings.

Actual mean energy flow of the breeding wren population in the study areas over a four year period was estimated at approximately 246 gcal/m² × day (Table 31). Correcting for a 70% assimilation efficiency (see page 47) an average value of 351 gcal/m² × day of food (about 62.6 mgm dry weight, or 186 mgm live weight of insects) was eaten by the population, an estimated food consumption representing 21% of the estimated standing crop of insects and spiders.

Because production rates of the insects and spiders in the salt marsh are not known, I do not know what the turnover rates of these populations are. Presumably, if the population turnover time is at least ten days, then a 10% consumption of the standing crop would

be tolerable. Removal of 20% of the insects and spiders each day would represent an extremely high predatory pressure of wrens on their food supply within the restricted territory.

I observed considerable movement of flying insects in the marsh. The presence of numerous webs of the orb weaver, *Eustala triflex* (Araneidae) in the shorter grass areas behind wren territories suggests that this spider was making its living from these moving insect populations. Thus movement of insects into wren territories from non-occupied areas might greatly augment the available food. It is quite possible that as wrens remove insects locally the latter are replaced rapidly by immigrants from the broad expanse of adjacent marsh not used by wrens. The elongated and narrow shape of territories increases the opportunity for immigration to occur across territorial boundaries. It is also possible that by using the sampling method I greatly underestimated the insect population density.

(2) *High Tides*

Animal populations living in physically "harsh" environments are often controlled by the physical factors (wind, desiccation, wave action, etc.) to which they are subjected. Prior to this study I thought that the wren population, living in a marine habitat characterized by wide diurnal tidal variations (2-3 meters), would be controlled primarily by this physical factor, if not by energy limitations. However, over the four year period mortality of eggs and nestlings from drowning tides was high during only one of these years (1960, see page 32) and this mortality (21%) was considerably lower than losses due to predation (63%). Thus high flood tides seem to exert a limiting effect upon production of young only at irregular intervals over a long period of time.

(3) *Predation*

Predation on eggs and young proved to be a major mortality factor during the nesting season. However, it was obvious that sufficient wrens were being produced each year to replace at least annual losses. In 1961, despite the poor fledgling production of 1960, the wren density (Table 14) in the study areas and in the watershed as a whole was similar to the previous two years. Population size remained relatively stable despite the marked variation in magnitude of predation, suggesting that predation is a locally important limiting factor but probably not an overall regulating factor.

(4) *Territoriality and Social Behavior*

Territoriality and the propensity of the marsh wren to aggregate into breeding colonies was discussed earlier (see page 69). A well developed territorial behavior effectively reduces intraspecific com-

petition and obviously controls population size in areas where available habitat is limiting. However, as already noted, about 50% of the potential tall marsh grass habitat is occupied each year during the breeding season. The observation that wrens, though strongly territorial, are attracted to each other may explain why some areas of suitable habitat are occupied and intensively utilized by groups of wrens while adjacent areas are not inhabited or are deserted early in the season.

Darling (1952) has hypothesized that contact between pairs at territorial boundaries provides the social stimulation necessary to bring birds of many species into reproductive condition. He bases his hypothesis on the observations of several authors (Nice, 1937, Armstrong, 1947, and Lack, 1948), who report the clumping of territories in what appears to be uniform habitat. Darling concludes that "the breeding territory has little to do with a sufficiency of feeding ground for raising the brood." Orians (1961) questions Darling's hypothesis as being too narrow and suggests that clumping might "result irrespective of any stimulatory effect of displays upon reproductive physiology" because "one of the cues which a bird uses to evaluate the suitability of habitats is the presence of other birds of the same species." Orians also cautions that what appears to be uniform to the human observer may not be uniform to the bird.

The vegetative uniformity within *Spartina alterniflora* zones impresses the observer (Kuenzler, 1959; Smalley, 1958; Teal, 1958, 1962). The various marsh types are the result of physical factors associated with tides, which exert a similar influence over wide areas. The fact that numerous pairs of wrens may occupy a particular area one season while only a few pairs, or none at all, will be present in the same area the next season would seem to indicate that social stimulation rather than micro-habitat differences account for the clumping of territories in the case of the marsh wren.

I conclude that territorial and colonial behavior of *griseus* plays an important role in limiting population size by insuring that some of the potential habitat is not occupied and is thus not subjected to heavy pressure on the food supply. These unoccupied areas of tall grass as well as the vast areas of shorter grass that lie inward from the streamside zone are hypothesized to be important as food reservoirs both during the nesting season and after the wrens disperse more widely throughout the marsh upon completion of breeding.

It might be suggested that the relatively small territory size (mean = 100 m²) maintained by *griseus* provides *a priori* evidence that food is not limiting. However, the nature of the habitat (long, narrow strips) is such that a wren probably could not maintain the integrity of its elongated territory if it were much larger. The territories of wrens in certain inland fresh water marshes are several times

as large as those of salt marsh wrens. Verner (1963) noted smaller territories (mean = 454 m²) being maintained by marsh wrens in the more productive marshes of eastern Washington than are maintained in less productive marshes near Seattle (mean = 1452 m²). Welter (1935) also observed that wrens in optimum habitat in Ithaca marshes maintained territories of 1300 m², less than half the size of territories in less favorable habitat.

These differences in size of territory between fresh water Long-billed Marsh Wrens and salt water wrens presumably may be a result of the less dense but more extensive tall-grass areas and the lower productivity of the inland marshes. The Sapelo marshes and estuaries have an estimated gross primary production of somewhere around 2000 g of dry organic matter/m² × yr and thus are among the most productive natural ecosystems in the world (Odum, 1961, Schelske and Odum, 1961). If a high rate of production and a continuous movement of food items is taking place throughout the marsh, as previously discussed, then it would be possible for the wren to exist on a smaller territory than would be possible if all food had to be produced within the narrow territorial boundaries, or if all of the marsh were occupied by wrens.

In summary, physical factors, such as high tides and weather, played a relatively minor role in population control, except at irregular intervals. Predation was the major mortality factor during the nesting season. It is probable that predation plays an important role in limiting population size by reducing fledgling production in local areas. No definite conclusions on food limitations can be made until energy flow of prey populations can be measured accurately. The combination of territorial and colonial behavior appears to be the mechanism that prevents overexploitation of the food supply.

ROLE OF THE WREN POPULATION IN THE ENERGY FLOW OF THE SALT MARSH ECOSYSTEM

(1) *Trophic Position*

As already noted *griseus* feeds upon animals at three different trophic levels. Table 41 presents a comparison of percent volume of herbivores (21 species), predators (30 species), and detritus feeders (16 species) found in 195 wren stomachs collected in the salt marsh during the breeding and winter seasons. Herbivores comprised approximately 52% of the diet by volume during the breeding season, and 62% in winter. Predators comprised 33% and 23% respectively, and detritus feeders approximately 12% during both seasons. Thus the marsh wren is primarily a secondary and tertiary consumer within the grazing food chain (Odum, 1962) of the salt marsh ecosystem.

TABLE 41

COMPARISON OF PERCENT VOLUME OF HERBIVORES, PREDATORS, AND DETRITUS FEEDERS IN 113 STOMACHS OF *T. p. griseus*, APRIL–AUGUST, AND 82 STOMACHS, SEPTEMBER–MARCH

	Trophic level:		<i>Herbivores^a</i>		<i>Predators^b</i>		<i>Detritus Feeders^c</i>	
	Season:	Breeding	Breeding	Winter	Breeding	Winter	Breeding	Winter
Hymenoptera		5.1 ^d		3.7	12.2	8.7		
Coleoptera		8.1		4.5	3.5	8.1		
Homoptera		13.0		40.1				
Diptera					2.6	0	6.3	7.7
Lepidoptera		14.6		2.9				
Hemiptera		5.4		10.0				
Orthoptera		5.6		0.8				
Spiders					15.1	6.2		
Other arthropods							1.8	0.9
Molluscs							3.5	3.9
Totals ^e		51.8		62.0	33.4	23.0	11.6	12.5

^a Approximately 21 species.

^b Approximately 30 species.

^c Approximately 16 species.

^d Two omnivorous species (ants).

^e Approximately 4% of food species with unknown diet.

(2) Impact Upon Food Supply

I have shown that *T. p. griseus* is at least a locally important predator both upon herbivorous insects feeding on *Spartina* and, especially, upon the hymenopterans and spiders that parasitize or prey on insects. Preliminary estimates of insect densities reveal high populations of the herbivore, *Prokelisia marginata*, and the omnivore, *Crematogaster clara*, both of which are important constituents of the wren's diet. Tentative analyses of the removal sweep data indicate high species-number diversity of parasitic wasps. The large numbers of Braconids, Chalcids, Ichneumonids, and Scelionids in the marsh are impressive. Although relatively few species of spiders are found in the salt marsh, relatively large numbers of individuals are present. The wren may be a major factor in the control of the secondary consumers among the arthropods.

Fig. 22 shows the relation of *T. p. griseus* to the energy flow of the salt marsh. Energy flow estimates of *Spartina* are from Teal (1962). The diagram shows that *griseus* obtains the major portion (85%) of its energy from the grazing food chain and only a small amount (12%) from the detritus chain, which is the major pathway of energy flow in the salt marsh ecosystem.

SUMMARY

1. Field and laboratory studies of the Long-billed Marsh Wren, *Telmatodytes palustris griseus*, were carried out from 1958 through 1963 on a resident population in the salt marshes of Sapelo Island, Georgia.

2. During the breeding season this race is found only in the narrow (1.5-5 m) bands of tall (1-3 m) *Spartina alterniflora*, which grows on the levees and streamsides of tidal creeks.

3. All breeding activities such as nest building and feeding and care of young take place within the territory established and defended by the male. Mean territory size was 100 m² (range: 30-242 m²).

4. Polygamy occurred in only 5% of the male population, while 4% of the males remained unmated.

5. Mean clutch size early in the season was 4.6 eggs/clutch while later clutches contained a mean of 3.8 eggs. Fifty-nine percent of the breeding nests contained 5 eggs/clutch; 32% contained 4 eggs/clutch; and 9% contained 3 eggs/clutch.

6. Mortality of eggs and young during the years 1958-1961 was 58.4%, 79.6%, 93.2%, and 85.2%, respectively. The majority of this loss was by predation—39.3%, 66.9%, 66.8%, and 80.8%, respectively.

7. Nesting success (percentage of eggs that fledged) was 42% in 1958, a value thought to represent an above average season because of

the relatively low mortality that occurred that year. In 1959-1961 nesting success was 20.0%, 6.8%, and 14.8%, respectively.

8. In 882 hectares (2190 acres) of *Spartina alterniflora* marshes in the Duplin River watershed, located west of Sapelo Island, the density of breeding wrens varied little from year to year and was estimated as follows: (1) Crude density, approximately 0.5 pairs/hectare (0.2 pairs/acre) of total marsh area, (2) ecological density of 45-56 pairs/hectare (18-23 pairs/acre) of suitable nesting area, and (3) utilized area density, 98-109 pairs/hectare (41-45 pairs/acre) of territorial area actually occupied.

9. Energy requirements of individual caged wrens were determined by two different methods: (1) Feeding experiments, which resulted in a mean of 11.8 Kcal/gross daily intake, of which 8.8 Kcal was metabolized (= assimilated)/bird $\times$ day for birds averaging 10.0 gm live weight; and (2) Oxygen consumption experiments resulting in a mean basal metabolic rate of 5.8 Kcal/bird $\times$ day (4.7 cc. O₂/gm $\times$ hr) and a rate in active birds of 8.2 Kcal/bird $\times$ day (7.0 cc O₂/gm $\times$ hr). It was concluded that measurement of respiratory energy by the oxygen respirometer is comparable to the results obtained by the feeding experiments, if the experimental birds are not restrained while in the chamber, and are not in a post absorptive condition.

10. Preliminary estimates of insect and spider populations in wren habitats indicated a mean density of over 500 individuals/m² (range: 50-2000) with considerable clumping of fulgorid and formicid populations. Mean dry biomass per square meter averaged approximately 300 mgm (range: 20-900) and mean energy content was 1500 gcal/m² (range 200-4200), which is only about four times the daily energy requirement of the wren population.

11. Stomach contents of 195 wrens collected throughout the year were analyzed to determine food items. Volume of contents ranged from 0.075 to 0.350 ml per stomach with a mean of 0.150 ml. Mean wet weight of 21 stomachs was 186 mgm. Hymenopterans and spiders were more frequent food items during the breeding season while fulgorids (Homoptera) and formicids (Hymenoptera) occurred with the highest frequencies in winter. Fulgorids comprised over 40% of the volume of winter stomachs while ants and spiders comprised 25% of the volume of stomachs during the breeding season.

12. Population energy flow was estimated by calculating the production and respiration of the standing crop biomass at weekly intervals throughout the breeding seasons. Mean annual production was estimated at approximately 4 gcal/m² $\times$ day (457 gcal/m² $\times$ yr). Mean respiratory energy flow was 242 gcal/m² $\times$ day and comprised most of the total energy flow. Mean energy flow over the four year period was 246 gcal/m² $\times$ day. Mean gross energy intake based on an assimilation efficiency of 70% for wild wrens on a diet of salt marsh

insects and spiders was estimated to be $351 \text{ gcal/m}^2 \times \text{day}$. Mean daily energy flow represented about 50% of the mean caloric value of the standing crop of wrens.

13. Of the possible limiting factors regulating population size, physical factors such as high tides or weather played a relatively minor role and are believed limiting only at irregular intervals. Predation was the major mortality factor during the nesting season and probably plays an important role in limiting nesting success (production) in local areas. The highly developed territorial and colonial behavior of the wren is the principal control of population size. By limiting the area occupied by breeding wrens to about half the potential habitat this colonial behavior reduces predation pressure upon the food supply in the unoccupied areas. These unoccupied areas, or buffer zones, are important as food reservoirs. It is suggested that wrens are able to maintain themselves on relatively small territories because of the regular immigration into their territories of insects from unoccupied potential wren habitat and from the other vast areas of very fertile marsh.

14. The diet of *griseus* consisted of approximately 58% (by volume) herbivores, 30% predators, and only 12% detritus feeders. Thus this wren is a secondary and tertiary consumer in the grazing food chain of the salt marsh ecosystem.

15. *T. p. griseus* is a locally important predator upon the herbivorous insects feeding on *Spartina alterniflora* and upon the hymenopterans and spiders that parasitize or prey on insects, and may be a major factor in the control of the secondary consumers among the arthropods of the grazing food chain.

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APPENDIX I

Area of male territories under observation during
the 1958-1961 breeding seasons

TABLE 42					
AREA OF MALE TERRITORIES DURING THE 1958-1961 BREEDING SEASONS					
Year	Location	Area (m ²)	Year	Location	Area (m ²)
1958	Study Area 1		1959	Study Area 4 (<i>cont.</i>)	
	Territory No. 1	56		11	48
	2	—		12	70
	3	61		13	130
	4	56		14	167
	5	56		15	121
	6	37		16	149
	7	46		17	149
	8	63		18	56
	9a ^a	61			
	9b	68	1959	Study Area 2	
	10	62		Territory No. 1	112
	11	93		2	167
				3	112
1958	Study Area 2			4	56
	Territory No. 1	136		5	121
	2	232		6	93
	3	232		7	195
	4	204		8	112
	5	139		9	112
	6	112		10	46
	7	184		11	37
	8	123		12	56
	9	135		13	56
	10	93		14	28
	11	186		15	56
	12	93		16	93
				17	70
1959	Study Area 4			18	84
	Territory No. 1	39 ^b		19	84
		77		20	56
	2	26		21	98
		60		22	37
	3	18			
		103	1960	Study Area 4	
	4	33		Territory No. 1	78
		92		2	60
	5	84		3	70
		195		4	77
	6	130		5	50
		242		6	69
	7	54		7	68
	8	102		8	112
	9	60		9	120
	10	43		10	230

TABLE 42 (<i>Continued</i>)					
Year	Location	Area (m ²)	Year	Location	Area (m ²)
1960	Study Area 4 (<i>cont.</i>)		1961	Study Area 4 (<i>cont.</i>)	
	11	50		5	80
	12	85		6	72
	13	75		7	128
				8	83
1960	Study Area 2			9	230
	Territory No. 1	126		10-11 ^c	175
	2	108		12	175
	3	75			
	4	90	1961	Study Area 2	
	5	120		Territory No. 1	180
	6	105		2	95
	7	58		3	70
	8	135		4	75
	9	50		5	94
	10	115		6	85
	11	76		7	132
	12	54		8	32
	13	95		9	50
	14	61		10-11 ^c	78
				12	60
1961	Study Area 4			13	40
	Territory No. 1	40		14	92
	2	84		15-16 ^c	145
	3	100		17-18 ^c	132
	4	74			

^a Territory 9 (1958) was occupied by a single male early in season but was divided between 2 males after 1 June.

^b The first area listed is inhabitable tall grass, utilized area. The second area is total maximum territory.

^c Two territories early in season, occupied by one male by June.

APPENDIX II

Summaries of wing lengths, weights, and caloric content
of wren tissue, feces, and food

TABLE 43				
SUMMARY OF WING LENGTHS AND WEIGHTS OF ADULT MALE WRENS (C.V. = COEFFICIENT OF VARIATION)				
	No. Ind.	Mean & Standard Error	S.D.	C.V.
Wing length (mm)	34	48.2 $\pm$ 0.3	1.7	3.5
Weights (gm)				
Fresh Wet Wt.	52	10.61 $\pm$ 0.10	0.7	7.0
Extracted Wet Wt. ^a	35	10.32 $\pm$ 0.13	0.8	7.7
Dry Wt.	41	3.61 $\pm$ 0.05	0.3	9.3
Water Wt.	40	6.77 $\pm$ 0.84	0.5	7.9
Fat Wt.	35	1.03 $\pm$ 0.04	0.2	6.3
Fat-Free Wt. ^b	35	9.29 $\pm$ 0.11	0.6	7.0
Lean Dry Wt.	35	2.60 $\pm$ 0.02	0.2	6.3
Ash Wt.	39	0.37 $\pm$ 0.004	0.02	6.2
Ash-free Dry Wt.	39	3.26 $\pm$ 0.05	0.3	10.2
Ash-free Lean Dry Wt.	35	2.24 $\pm$ 0.02	0.1	6.7
Ash-% Dry Wt.	39	10.2 $\pm$ 0.2	0.9	9.1
Ash-% Lean Dry Wt.	35	14.0 $\pm$ 0.1	0.7	5.0
Water Index ^c	35	2.58 $\pm$ 0.02	0.1	5.6
Fat Index ^d	35	0.39 $\pm$ 0.01	0.07	19.0

^a Fresh wet weight minus stomach weight. All other weights are determined from this weight.

^b Extracted wet weight minus fat weight.

^c Water weight divided by lean dry weight.

^d Fat weight divided by lean dry weight.

TABLE 44

SUMMARY OF WING LENGTHS AND WEIGHTS OF ADULT FEMALE MARSH WRENS
(C.V. = COEFFICIENT OF VARIATION)

	No. Ind.	Mean & Standard Error	S.D.	C.V.
Wing length (mm)	19	45.2 $\pm$ 0.5	2.1	4.6
Weights (gm)				
Fresh Wet Wt.	25	9.41 $\pm$ 0.22	1.1	11.5
Extracted Wet Wt. ^a	19	9.29 $\pm$ 0.25	1.0	11.3
Dry Wt.	24	3.14 $\pm$ 0.10	0.5	14.9
Water Wt.	24	6.03 $\pm$ 0.15	0.7	11.7
Fat Wt.	18	1.04 $\pm$ 0.06	0.3	11.0
Fat-free Wt. ^b	18	8.28 $\pm$ 0.22	0.9	11.2
Lean Dry Wt.	18	2.22 $\pm$ 0.06	0.3	11.8
Ash Wt.	21	0.33 $\pm$ 0.007	0.03	6.0
Ash-free Dry Wt.	21	2.86 $\pm$ 0.10	0.4	15.8
Ash-free Lean Dry Wt.	17	1.80 $\pm$ 0.13	0.5	28.8
Ash-% Dry Wt.	21	10.5 $\pm$ 0.3	1.4	13.4
Ash-% Lean Dry Wt.	17	14.6 $\pm$ 0.2	1.0	7.1
Water Index ^c	18	2.70 $\pm$ 0.07	0.3	25.0
Fat Index ^d	18	0.47 $\pm$ 0.007	0.03	6.0

^a Fresh wet weight minus stomach weight. All other weights are determined from this weight.

^b Extracted wet weight minus fat weight.

^c Water weight divided by lean dry weight.

^d Fat weight divided by lean dry weight.

TABLE 45
SUMMARY OF WING LENGTHS AND WEIGHTS OF IMMATURE
MALE AND FEMALE MARSH WRENS
(C.V. = COEFFICIENT OF VARIATION)

	No. Ind.	Mean & Standard Error	S.D.	C.V.
Wing length (mm)	34	45.6 $\pm$ 0.4	2.1	4.6
Weights (gm)				
Fresh Wt.	56	9.44 $\pm$ 0.21	1.6	16.9
Extracted Wet Wt. ^a	34	8.92 $\pm$ 0.16	0.9	10.2
Dry Wt.	35	3.23 $\pm$ 0.07	0.4	12.6
Water Wt.	35	5.63 $\pm$ 0.12	0.8	14.2
Fat Wt.	34	1.04 $\pm$ 0.04	0.2	20.6
Fat-Free Wt. ^b	34	7.88 $\pm$ 0.14	0.8	10.6
Lean Dry Wt.	34	2.20 $\pm$ 0.05	0.3	13.4
Ash Wt.	34	0.30 $\pm$ 0.006	0.035	11.9
Ash-free Dry Wt.	34	2.94 $\pm$ 0.06	0.4	13.0
Ash-free Lean Dry Wt.	34	1.90 $\pm$ 0.04	0.3	13.7
Ash-% Dry Wt.	34	9.19 $\pm$ 0.14	0.8	8.7
Ash-% Lean Dry Wt.	34	13.54 $\pm$ 0.14	0.8	6.0
Water Index ^c	34	2.57 $\pm$ 0.07	0.4	15.4
Fat Index ^d	34	0.48 $\pm$ 0.02	0.1	21.4

^a Fresh wet weight minus stomach weight. All other weights are determined from this weight.

^b Extracted wet weight minus fat weight.

^c Water weight divided by lean dry weight.

^d Fat weight divided by lean dry weight.

TABLE 46

CALORIC CONTENT OF FAT-EXTRACTED WILD WRENS

Lab. No.	Sex/Age	Lean Dry Weight (Gm)	Fat Weight (Gm)	Ash Weight (Gm)	Ash-free Lean Dry Calories	Total Fat Calories ^a	Total Kcal/bird	Total Ash-free Kcal/gm
18	M Ad	2.50	1.05	.36	10.57	9.45	20.02	6.28
10	M Ad	2.64	1.20	.41	12.24	10.80	23.04	6.72
123	M Ad	2.90	1.63	.37	13.85	14.67	28.52	6.84
116	M Ad	2.79	1.03	.36	13.20	9.27	22.47	6.51
88	M Ad	2.55	1.11	.36	11.43	9.99	21.42	6.51
45	M Ad	2.80	0.95	.42	12.81	8.55	21.36	6.41
75	M Ad	2.51	0.95	.33	11.79	8.55	20.34	6.50
108	M Ad	2.64	1.08	.36	12.29	9.72	22.01	6.57
69	M Ad	2.71	0.82	.36	12.83	7.38	20.21	6.38
4	M Ad	2.40	0.82	.38	10.34	7.38	17.72	6.24
38	M Ad	2.75	1.57	.36	12.65	14.13	26.78	6.76
118	F Ad	2.37	0.81	.33	11.22	7.29	18.51	6.49
44	F Ad	2.44	1.14	.33	10.78	10.26	21.04	6.52
84	F Ad	2.36	1.03	.34	10.34	9.27	19.61	6.43
121	F Ad	1.86	1.07	.30	8.39	9.63	18.02	6.85
73	F Ad	2.18	1.10	.31	10.32	9.90	20.23	6.81
86	F Ad	1.98	0.71	.30	8.97	6.39	15.36	6.43
53	F Ad	2.63	1.91	.34	12.38	17.19	25.57	7.04
83	F Im	2.04	1.45	.28	8.55	13.05	21.60	6.73
65	F Im	2.33	0.94	.31	10.83	8.46	19.29	6.96
16	M Im	2.19	1.10	.28	8.86	9.90	18.76	6.26
85	M Im	1.87	0.87	.27	8.59	7.83	16.42	6.65
80	M Im	1.72	0.85	.22	7.99	7.65	15.64	6.66

^a Fat = 9.0 Kcal/gm.

TABLE 46 (*Continued*)

Lab No.	Sex/Age	Lean Dry Weight (Gm)	Fat Weight (Gm)	Ash Weight (Gm)	Ash-free Lean Dry Calories	Total Fat Calories ^a	Total Kcal/bird	Total Ash-free Kcal/gm
41	M Im	2.36	0.78	.32	11.19	7.02	18.21	6.46
51	M Im	2.68	1.40	.34	12.44	12.60	25.04	6.71
36	M Im	2.11	1.52	.29	8.96	13.68	22.64	6.78
71	— Fledgling	1.45	1.12	.21	6.23	10.08	16.31	6.91
8	F Fledgling	1.83	0.90	.24	8.03	8.10	16.13	6.50
125	M Fledgling	1.79	0.91	.25	8.23	8.19	16.42	6.70

^a Fat = 9.0 Kcal/gm.

TABLE 47

CALORIC CONTENT OF WHOLE (NON-FAT EXTRACTED) ADULTS AND FLEDGLINGS

Lab. No.	Sex/Age		Dry Weight (Gm)	Ash Weight (Gm)	Total Ash-free Dry Calories	Ash-free Kcal/gm
C-7	M	Ad	3.29	.42	17.35	6.04
C-8	M	Ad	3.48	.41	18.90	6.16
C-9	M	Ad	3.64	.41	20.97	6.49
C-12	M	Ad	3.76	.38	21.75	6.43
C-2	F	Ad	3.05	.35	15.62	5.79
C-13	F	Ad	2.59	.37	13.43	6.05
C-6	F	Ad	2.56	.34	13.58	6.12
C-10	F	Ad	2.89	.34	16.06	6.30
C-3	—	Im	2.91	.28	17.34	6.59
C-11	Fledgling		3.39	.25	21.10	6.72
C-1	9 days-Fldg.		2.35	.23	12.97	6.12
C-4	9 days-Fldg.		2.14	.21	11.93	6.18
C-5	9 days-Fldg.		2.17	.21	12.45	6.35

TABLE 48
CALORIC CONTENT OF EGGS AND NESTLINGS OF *T. p. griseus*

Lab No.	Individuals per sample	Incubation or Nestling Age (in days)	Dry Weight (Gm)	Ash Weight (Gm)	Total Ash-free Dry Calories	Ash-free Kcal/gm
Eggs						
Eg-1	10	Fresh-2	2.90	1.03	13.12	7.02
Eg-2	14	Fresh-2	3.78	1.34	16.47	6.75
Eg-3	12	1-5	3.20	1.13	13.87	6.70
Eg-4	14	5-8	3.71	1.31	16.08	6.70
Eg-5	14	8-13	3.53	1.25	14.91	6.54
Nestlings						
Ns-1	11	1-2	2.21	0.25	11.43	5.83
Ns-2	5	5	2.81	0.23	15.84	6.14
Ns-3	2	5-9	3.36	0.29	18.88	6.13
Ns-4	2	5-9	2.90	0.23	16.56	6.18

TABLE 49
CALORIC CONTENT OF FAT-EXTRACTED CAPTIVE WRENS

Lab No. ^a	Sex/Age	Lean Dry Weight (Gm)	Fat Weight (Gm)	Ash Weight (Gm)	Ash-free Lean Dry Calories	Total Fat Calories ^b	Total Kcal/bird	Total Ash-free Kcal/gm
110	M Ad	2.64	0.92	.33	12.47	8.28	20.75	6.42
113	M Ad	2.58	1.55	.38	11.79	13.95	25.74	6.86
115	M Ad	2.75	1.45	.39	12.95	13.05	26.00	6.82
114	F Ad	2.08	1.29	.26	9.45	11.61	21.06	6.77
112	F Ad	2.32	1.09	.27	10.87	9.81	20.68	6.63

^a The individual number of each wren in the order presented above is: 86, 92, 12, 11, 91.

^b Fat = 9.0 Kcal/gm.

TABLE 50 DRY WEIGHT, ASH WEIGHT, AND CALORIC CONTENT OF WREN FOOD (MEALWORMS AND WREN MIXTURE)			
	Percent Dry Weight (of wet wt.)	Percent Ash Weight (of dry wt.)	Kcal/gm (Ash-free dry wt.)
Mealworms	38.00	97.50	6.569
Wren Mixture			
Batch No. 2	54.79	95.00	5.635
No. 3	53.24	94.94	5.679
No. 4	52.05	95.10	5.811
No. 5	51.27	95.60	6.108
No. 6	51.22	95.08	5.673
No. 7	52.01	95.16	5.540
No. 8	51.72	95.07	5.765
No. 9	52.82	94.78	5.574

TABLE 51
CALORIC CONTENT OF FECES OF WRENS ON EXPERIMENTAL DIET

Wren No.	Wren Mixture Batch Number	Kcal/gm (ash-free dry weight)
84m	3	3.670
	3	3.636
	8	3.667
85m	2	3.528
	3	3.702
	3	3.706
	5	3.644
	8	3.720
86m	3	3.561
	5	3.530
	7	3.555
87m	2	3.571
	3	3.433
	3	3.586
	5	3.620
	7	3.570
92m	2	3.600
	3	3.682
	5	3.724
	7	3.584
98m	2	3.534
	3	3.702
	3	3.563
12m	7	3.644
83f	3	3.578
	5	3.596
	7	3.594
91f	3	3.655
	5	3.533
	8	3.646
11f	7	3.614
(6 wrens)	9	3.795

TABLE 52			
DRY WEIGHTS OF MISCELLANEOUS SALT MARSH INSECTS AND SPIDERS			
	Total Nr.	Total Dry Wt. (mgm)	Dry Wt. per Individual (mgm)
Hymenoptera			
<i>Crematogaster clara</i>			
Workers	100	39.9	0.4
Queens	5	7.5	1.5
<i>Eurytoma</i> sp.	28	14.3	0.5
<i>Telenomus poici</i>	3	0.4	0.1
Eupelmidae (one species)	30	3.0	0.1
<i>Chelonus</i> sp.	1		1.0
Mixed small wasps	54	15.4	0.3
Coleoptera			
<i>Collops subtropicus</i>	2	8.1	4.0
Melyridae larva	1		1.7
<i>Isohydnocera tabida</i>	6	7.1	1.2
<i>Mordellistena nigricans</i>	11	7.1	0.6
Anthribidae	4	2.4	0.6
Anthribidae	5	9.9	1.9
Curculionidae	14	29.0	2.1
<i>Orthoperis</i> sp.	7	0.5	0.1
Diptera			
Dolichopodidae	48	27.9	0.6
Dolichopodidae	4	2.2	0.6
<i>Dimecoenia spinosa</i>	30	46.7	1.6
<i>Dimecoenia spinosa</i>	8	18.4	2.3
<i>Dimecoenia spinosa</i>	4	6.5	1.6
<i>Notiphila bispinosa</i>	5	5.4	1.1
<i>Hoplodictya setosa</i>	29	88.8	3.1
<i>Hoplodictya setosa</i>	5	17.6	3.5
<i>Dictya</i> sp.	3	11.5	3.8
<i>Chaetopsis aenea</i>	8	22.9	2.9
<i>Chaetopsis aenea</i>	36	89.5	2.4
<i>Chaetopsis apicalis</i>	64	53.5	0.8
<i>Chaetopsis apicalis</i>	13	9.0	0.7
<i>Chaetopsis apicalis</i>	120	120.6	1.0
<i>Elachiptera</i> sp.	3	0.7	0.2
<i>Elachiptera</i> sp.	19	7.4	0.3
<i>Elachiptera</i> sp.	9	4.0	0.4
Sarcophagidae	2	10.4	5.2
<i>Oscinella insularis</i>	42	5.4	0.1
<i>Oscinella insularis</i>	53	5.7	0.1
<i>Psilopa compta</i>	7	2.2	0.3

TABLE 52 (*Continued*)

	Total Nr.	Total Dry Wt. (mgm)	Dry Wt. per Individual (mgm)
Homoptera			
<i>Prokelisia marginata</i>	200	92.7	0.5
<i>Prokelisia marginata</i>	200	76.0	0.4
<i>Prokelisia marginata</i>	400	150.4	0.4
<i>Prokelisia marginata</i>	18	6.0	0.3
Hemiptera			
<i>Ischnodemus badius</i>	50	127.0	2.5
<i>Trigonotylus</i> sp.	61	84.0	1.4
<i>Trigonotylus</i> (nymphs)	9	6.4	0.7
Lepidoptera			
One larva (8 mm)	1		11.3
Geometridae	3	65.0	21.6
Spiders			
Mixed sample	26	103.7	3.9
Mixed sample	30	88.1	2.9
Mixed sample	12	28.7	2.3
<i>Marpissa bina</i>	1		11.7
<i>Marpissa pikei</i>	2	4.7	2.3
<i>Clubiona littoralis</i>	4	21.8	5.4
<i>Thanatidius</i> sp.	1		13.9

APPENDIX III

Summaries of feeding experiments, oxygen consumption,
and environmental temperatures

TABLE 53

ANNUAL SUMMARY OF MEAN DAILY ENERGY INTAKE, LOSS, ASSIMILATION, AND RESPIRATION FOR EACH CAPTIVE WREN.
(C.V. = COEFFICIENT OF VARIATION; A/I = ASSIMILATION/INTAKE = ASSIMILATION EFFICIENCY; N = NUMBER OF WEEKS OF MEASUREMENTS)

Wren No.	Weight (Gm)	Gross Intake	Excreta Loss	Assimilation Kcal/day	Assimilation Gcal/gm × hr	Energy Stored	Energy Catabolized	Respiration Kcal/day	Respiration Gcal/gm × hr	A/I
12m (N = 6)										
$\overline{M}$	10.0	13.5	2.9	10.6	44	2.6	11.3	10.5	43	78.3
S.E.	± 0.1	± 0.3	± 0.2	± 0.3	± 1			± 0.4	± 2	± 0.9
S.D.	0.3	0.9	0.4	0.7	5			0.8	3	2.0
C.V.	2.6	6.8	15.2	6.5	4.9			8.0	8.1	2.5
84m (N = 15)										
$\overline{M}$	9.8	11.7	2.6	9.0	38	9.9	13.0	9.0	38	77.4
S.E.	± 0.1	± 0.3	± 0.1	± 0.2	± 1			± 0.2	± 1	± 1.4
S.D.	0.2	1.2	0.4	0.9	4			0.9	5	1.6
C.V.	2.6	10.0	1.5	9.8	11.4			10.3	12.1	2.1
85m (N = 26)										
$\overline{M}$	10.4	11.2	2.6	8.6	35	13.8	13.0	8.6	35	76.7
S.E.	± 0.1	± 0.2	± 0.1	± 0.2	± 1			± 0.2	± 1	± 0.4
S.D.	0.6	1.3	0.4	0.9	3			0.9	3	2.2
C.V.	5.3	11.2	16.1	10.8	9.9			10.8	9.9	2.9
86m (N = 19)										
$\overline{M}$	9.4	12.4	3.1	9.3	41	10.8	15.2	9.3	41	74.8
S.E.	± 0.8	± 0.3	± 0.1	± 0.2	± 1			± 0.2	± 1	± 0.5
S.D.	0.3	1.3	0.5	0.9	3			0.7	3	2.0
C.V.	3.4	10.7	16.8	9.6	9.3			8.0	7.2	2.7

TABLE 53 (Continued)

Wren No.	Weight (Gm)	Gross Intake	Exereta Loss	Assimilation		Energy Stored	Energy Catabolized	Respiration		A/I
				Kcal/day	Geal/gm × hr			Kcal/day	Geal/gm × hr	
87m (N = 30)										
$\overline{M}$	11.2	11.8	2.7	9.0	33			8.9	33	76.6
S.E.	± 0.1	± 0.2	± 0.04	± 0.1	± 0.4			± 0.1	± 0.4	± 0.3
S.D.	0.8	1.0	0.2	0.8	2			0.7	2	1.8
C.V.	7.0	8.6	8.8	8.8	6.7			8.2	6.7	2.4
92m (N = 23)										
$\overline{M}$	10.6	12.4	3.0	9.3	3.6			9.4	37	75.3
S.E.	± 0.1	± 0.2	± 0.1	± 0.1	± 1			± 0.1	± 1	± 0.4
S.D.	0.5	0.9	0.4	0.7	3			0.7	2	2.0
C.V.	5.0	7.4	12.3	7.2	7.3			7.2	7.0	2.7
98m (N = 16)										
$\overline{M}$	9.8	10.8	2.6	8.3	35			8.3	35	76.2
S.E.	± 0.2	± 0.2	± 0.1	± 0.2	± 1			± 0.2	± 1	± 0.4
S.D.	0.6	1.0	0.3	0.8	2			0.8	2	1.4
C.V.	6.7	8.9	10.3	9.2	7.2			9.3	7.1	1.8
11f (N = 6)										
$\overline{M}$	8.0	11.8	3.1	8.6	45			8.7	46	73.5
S.E.	± 0.1	± 0.2	± 0.1	± 0.1	± 1			± 0.1	± 1	± 0.6
S.D.	0.3	0.5	0.3	0.3	2			0.3	2	1.3
C.V.	3.3	4.3	8.4	3.5	5.1			3.4	3.5	1.8

TABLE 53 (Continued)									
Wren No.	Weight (Gm)	Gross Intake	Excreta Loss	Assimilation Kcal/day	Energy Stored gm × hr	Energy Catabolized	Respiration Kcal/day	Respiration Gcal/ gm × hr	A/I
83f (N = 18)									
$\overline{M}$	8.8	10.5	2.4	8.0	38		8.0	38	76.9
S.E.	± 0.2	± 0.3	± 0.1	± 0.2	± 1		± 0.2	± 1	± 0.4
S.D.	0.3	1.0	0.5	0.8	4		0.7	3	2.6
C.V.	3.4	10.1	22.0	9.6	9.4		9.1	8.7	2.1
91f (N = 14)									
$\overline{M}$	9.1	10.4	2.4	8.0	36	4.3	8.1	37	77.1
S.E.	± 0.1	± 0.3	± 0.1	± 0.2	± 1		± 0.2	± 1	± 0.7
S.D.	0.4	1.1	0.4	0.8	3		0.8	1	2.5
C.V.	2.0	10.8	19.1	9.7	9.2	8.3	9.6	8.9	3.3

TABLE 54 BODY WEIGHTS, OXYGEN CONSUMPTION AND HEAT PRODUCTION OF CAPTIVE WRENS UNDER NEAR-BASAL CONDITIONS WITHIN ZONE OF THERMONEUTRALITY				
Wren No.	Weight (Gm)	Ambient Temp. °C	Ce O ₂ / gm × hr	Kcal/ bird × day
12m	12.25	35°	5.4	7.76
	12.33	30°	5.3	7.76
	10.03	23°	4.8	5.68
84m	9.82	27°	3.7	4.23
	9.15	26°	4.6	4.96
85m	10.74	27°	4.6	5.80
	11.54	28°	4.2	5.68
86m	8.94	26°	3.0	2.82
87m	11.38	35°	4.7	6.35
	11.08	30°	5.9	7.77
	10.60	27.5°	6.2	7.76
	11.58	23°	4.1	5.68
92m	10.91	27°	3.3	4.23
	11.58	26°	4.6	6.38
	11.88	25°	4.5	6.39
	11.57	23°	5.7	7.80
	11.58	23.5°	4.1	5.68
98m	9.64	27.5°	5.0	5.67
	10.62	26°	5.0	6.35
91f	10.12	35°	4.7	5.65
	8.54	27°	4.2	4.25
	8.88	25°	5.3	5.60
	8.76	25°	4.8	4.96
	11.79	25°	4.6	6.39
	10.42	24°	4.6	5.68
	9.91	25°	5.4	6.39
	10.29	23°	5.2	6.39
83f	9.34	31°	3.8	4.23
	8.54	25.5°	4.2	4.23
	8.86	25°	5.4	5.68
N =	30		30	30
$\overline{M}$ =	10.42		4.7	5.81
S.E. =	± 0.22		± 0.1	± 0.23
S.D. =	1.18		0.7	1.24
C.V. =	11.34		15.6	21.3

TABLE 55							
NEAR-BASAL RATES OF OXYGEN CONSUMPTION (Cc O ₂ /GM × HR) ^a							
Interval °C	5–15°	15–20°	20–25°	25–30°	30–35°	35–40°	40–45°
	8.3	6.7	5.7	4.2	3.8	5.5	6.4
	7.8	7.2	5.2	4.6	4.7	7.6	6.5
	10.6	9.6	4.8	4.6	4.7	7.9	7.5
	9.0	5.3	4.1	5.0	5.4		7.5
		6.1	4.1	3.3			7.4
		7.4	4.6	3.7			
		6.4	4.5	4.2			
			4.6	4.6			
			4.8	5.0			
			5.3	6.2			
			5.4	5.3			
			5.4	5.9			
				3.0			
				4.2			

^a See Table 26 for statistical summary and Fig. 19 for graphic illustration of these data.

TABLE 56				
BODY WEIGHTS, OXYGEN CONSUMPTION, AND HEAT PRODUCTION OF ACTIVE CAPTIVE WRENS WITHIN ZONE OF THERMONEUTRALITY				
Wren No.	Weight (Gm)	Ambient Temp. °C.	Ce O ₂ /gm × hr	Kcal/bird × day
12m	12.12	24°	5.9	8.50
84m	10.18	28°	7.6	9.22
	9.36	25°	8.9	9.88
	9.36	25°	7.4	8.23
	9.63	25°	5.6	6.38
85m	9.85	25°	6.7	7.78
86m	9.26	26°	9.0	9.88
	9.61	23°	6.8	7.77
87m	11.41	33.5°	6.3	8.47
	11.22	23°	7.0	9.23
	10.28	25°	8.7	10.58
	11.29	25°	6.9	9.22
	11.46	25°	6.3	8.50
	11.54	25°	5.7	7.80
92m	12.20	25.5°	5.4	7.80
	9.44	25°	5.7	6.38
	10.59	25°	6.2	7.80
	10.36	23.5°	5.8	7.07
83f	9.12	23°	5.9	6.36
	9.16	24.5°	6.5	7.10
	9.22	27°	6.5	7.10
91f	8.83	25°	6.8	7.10
	9.58	27°	8.7	9.91
11f	8.72	26°	8.9	9.23
	8.90	24.5°	8.1	8.52
	8.26	25°	7.3	7.10
	9.04	23.5°	8.6	9.23
	8.36	23°	7.9	7.81
N =	28		28	28
$\overline{M}$ =	9.94		7.0	8.21
S.E. =	± 0.2		± 0.2	± 0.22
S.D. =	1.1		1.2	1.2
C.V. =	11.4		16.4	14.2

TABLE 57
 MEAN MAXIMUM, MINIMUM, AND MONTHLY MEAN TEMPERATURES (°C) AT SAPELO ISLAND, GEORGIA, 1958-1961
 (UNITED STATES WEATHER BUREAU DATA)

Month	1958			1959			1960			1961		
	Mean		Mean	Mean		Mean	Mean		Mean	Mean		Mean
	Max	Min		Max	Min		Max	Min		Max	Min	
Jan.	12.4	2.4	7.4	15.4	4.7	10.1	16.5	6.4	11.5	14.6	3.7	9.2
Feb.	14.2	1.2	7.7	18.4	10.3	14.4	16.6	5.9	11.3	19.0	8.2	13.6
Mar.	17.9	8.3	13.1	19.4	9.8	14.6	16.0	5.1	10.5	23.8	12.2	18.0
Apr.	24.0	14.3	19.2	25.4	15.1	20.3	24.3	14.3	19.3	23.3	11.6	17.4
May	26.4	18.7	22.6	29.2	19.8	24.5	27.7	17.0	22.5	27.2	17.5	22.4
June	30.6	22.4	26.5	31.0	21.5	26.3	30.5	21.3	26.0	29.5	20.7	25.1
July	31.5	23.6	27.6	31.7	22.4	27.1	32.3	25.9	29.1	32.2	22.1	27.3
Aug.	32.2	22.6	27.4	32.5	24.7	28.6	31.8	24.2	28.0	30.7	22.8	26.8
Sep.	30.3	21.9	26.1	29.4	22.2	25.9	29.5	22.7	26.1	29.9	22.6	26.3
Oct.	24.0	16.2	20.1	26.4	19.7	23.1	26.9	18.0	22.4	25.4	15.2	20.3
Nov.	22.9	13.9	18.4	20.3	11.2	15.8	22.3	12.0	17.1	22.4	12.3	17.4
Dec.	16.8	6.0	11.4	15.7	6.9	11.3	15.1	2.4	8.7	18.8	7.2	13.1

APPENDIX IV

Summaries of biomass, energy content, respiration,
and production of marsh wrens

TABLE 58
BIOMASS (STANDING CROP) OF WRENS (ADULTS, EGGS, YOUNG)
IN MGM ASH-FREE DRY WEIGHT PER M² OF INHABITED MARSH

Date	1958	1959	1960*	1961
Mar. 27-Apr. 3		60		68
Apr. 4-10		60		69
Apr. 11-17	54	64		69
Apr. 18-24	54	67	72	70
Apr. 25-May 1	58	70		73
May 2-8	60	92	74	77
May 9-15	71	101		79
May 16-22	80	94	75	81
May 23-29	83	96		86
May 30-June 5	88	92		80
June 6-12	93	96	78	84
June 13-19	88	104	81	84
June 20-26	90	105	78	83
June 27-July 3	93	109	75	84
July 4-10	93	107	74	86
July 11-17	91	110	74	92
July 18-24	96	110	72	92
July 25-31	93	109	76	93
Aug. 1-7	94	108	78	96
Aug. 8-14	102	105	80	97
Aug. 15-21	103		83	94
Aug. 22-28	104		80	

* Observations not weekly during April and May, 1960.

TABLE 59
ENERGY CONTENT OF STANDING CROP OF WRENS IN GCAL/M²
OF INHABITED MARSH, 1958-1961
(SEE FIG. 18 FOR GRAPH.)

Dates	1958	1959	1960 ^a	1961
Mar. 27-Apr. 3		397		450
Apr. 4-10		398		453
Apr. 11-17	358	425		458
Apr. 18-24	359	445	477	460
Apr. 25-May 1	385	464		485
May 2-8	394	595	488	507
May 9-15	460	664		522
May 16-22	522	621	497	536
May 23-29	546	631		562
May 30-June 5	575	611		527
June 6-12	610	632	515	554
June 13-19	585	679	538	556
June 20-26	590	690	513	550
June 27-July 3	610	719	499	552
July 4-10	615	707	492	564
July 11-17	592	726	487	560
July 18-24	628	721	478	609
July 25-31	615	721	498	611
Aug. 1-7	617	712	515	631
Aug. 8-14	665	692	527	641
Aug. 15-21	679		550	618
Aug. 22-28	683		527	

^a Observations not weekly during April and May, 1960.

TABLE 60
PRODUCTION OF WREN BIOMASS IN GCAL/M², 1958-1961

Date	1958	1959	1960	1961
Apr. 4-10		1		3
Apr. 11-17		21		5
Apr. 18-24	2	14		5
Apr. 25-May 1	26	28		32
May 2-8	16	126	10	23
May 9-15	72	87		28
May 16-22	76	19		56
May 23-29	31	49	20	66
May 30-June 5	63	12		21
June 6-12	75	46	28	49
June 13-19	14	63	36	16
June 20-26	35	50	20	22
June 27-July 3	54	48	10	22
July 4-10	24	16	19	30
July 11-17	4	29	23	53
July 18-24	54	30	12	49
July 25-31	13	9	32	15
Aug. 1-7	21	5	37	31
Aug. 8-14	67	10	19	24
Aug. 15-21	33		46	1
Aug. 22-28	43		20	

TABLE 61
RESPIRATION IN GCAL/M² OF STANDING CROP OF NESTLINGS, 1958-1961

Date	1958	1959	1960	1961
Apr. 25-May 1		7		
May 2-8		51		1
May 9-15	31	83		4
May 16-22	53	34		19
May 23-29	67	12		28
May 30-June 5	26	0		21
June 6-12	46	11		15
June 13-19	13	29		24
June 20-26	17	12		8
June 27-July 3	28	19		6
July 4-10	33	16	3	18
July 11-17	4	12	3	25
July 18-24	16	14	2	31
July 25-31	16	6	8	17
Aug. 1-7	10	2	21	17
Aug. 8-14	28		23	21
Aug. 15-21	27		30	

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FIGURE 1. *Spartina alterniflora* marsh in the Duplin River watershed. Marsh wrens inhabit the streamside marsh occurring along the edges of Barn Creek shown here. (Photo courtesy of E. P. Odum)

ZONATION - GEORGIA SPARTINA MARSHES

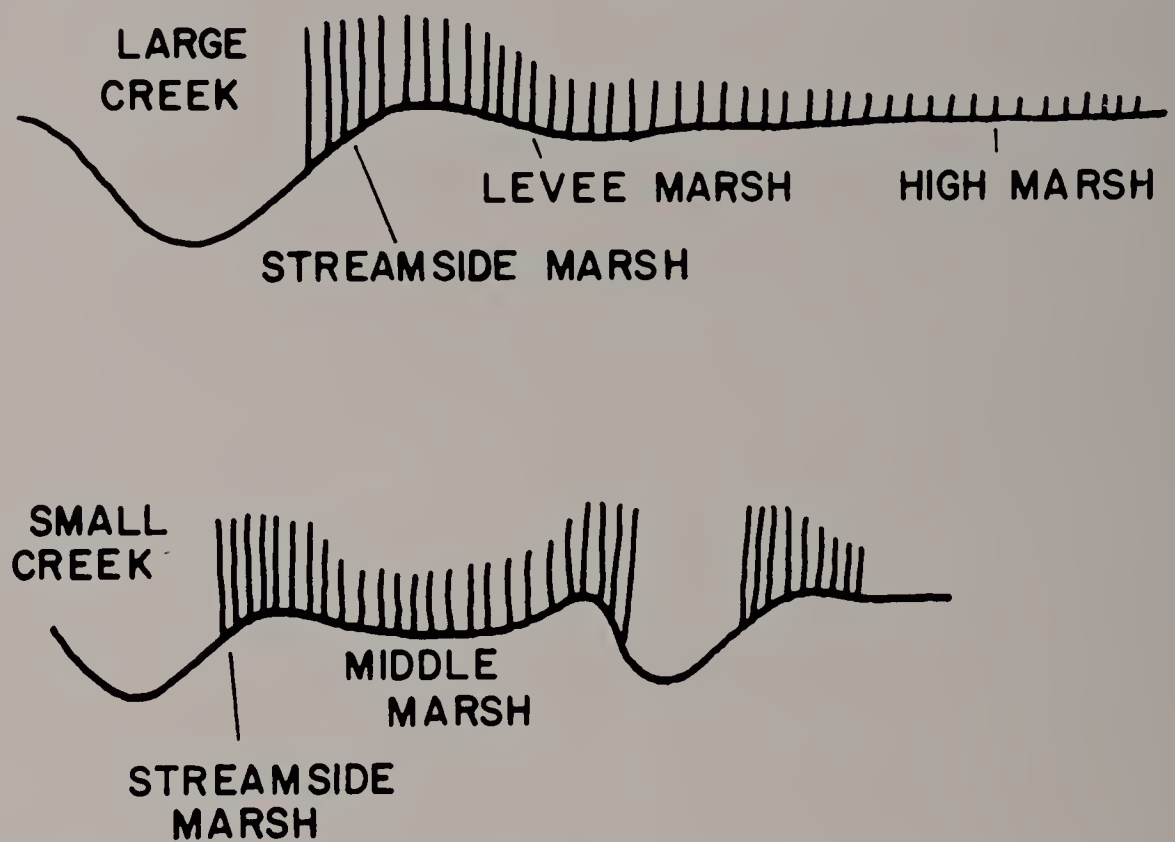


FIGURE 2. Zonation of the *Spartina* marshes at Sapelo Island, Georgia. Note the four types of marsh.

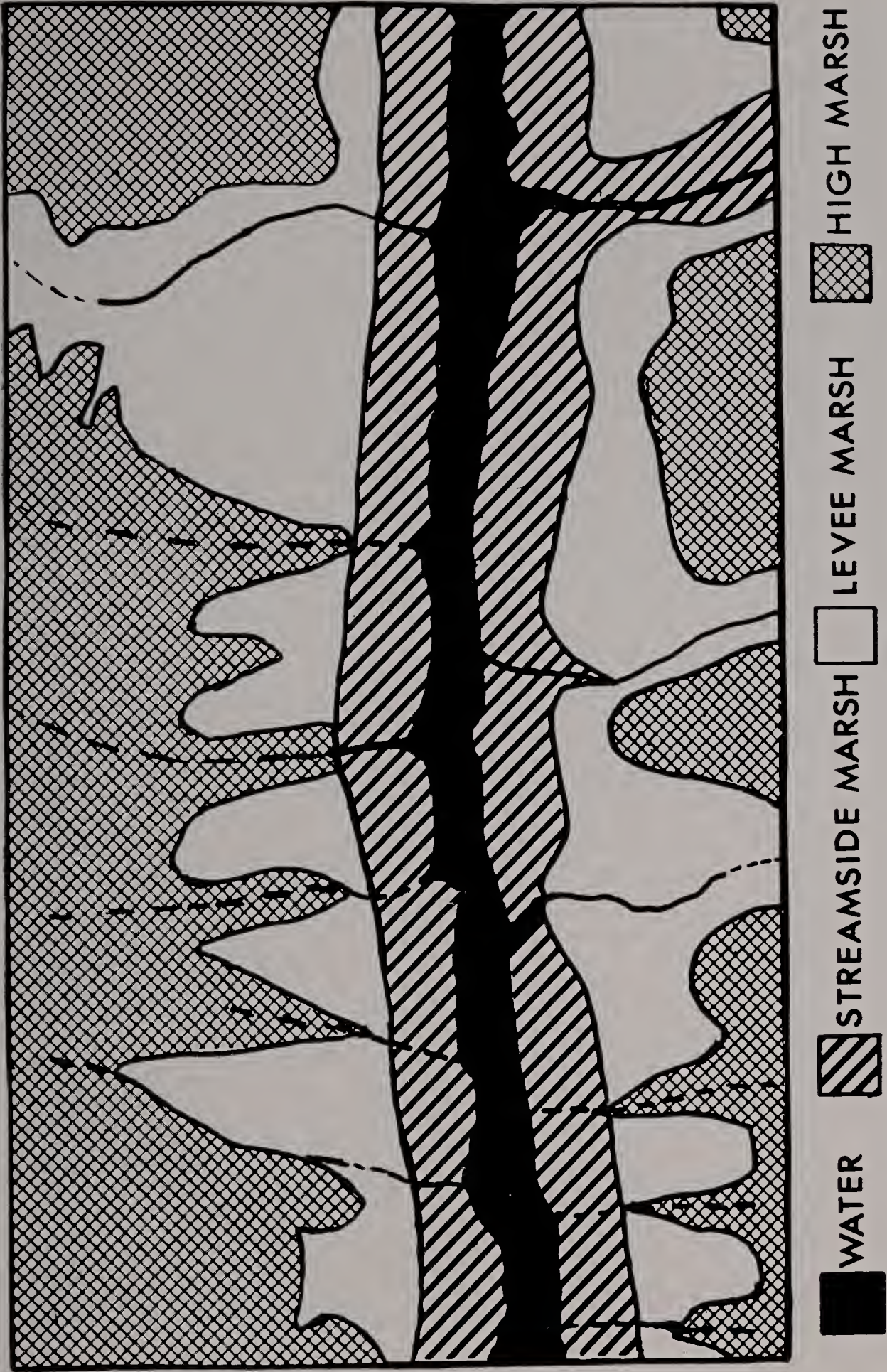


FIGURE 3. Diagram of an aerial kodachrome showing drainage pattern and marsh types in wren habitats. Scale, approximately 1:1100. (From Smalley, 1959)

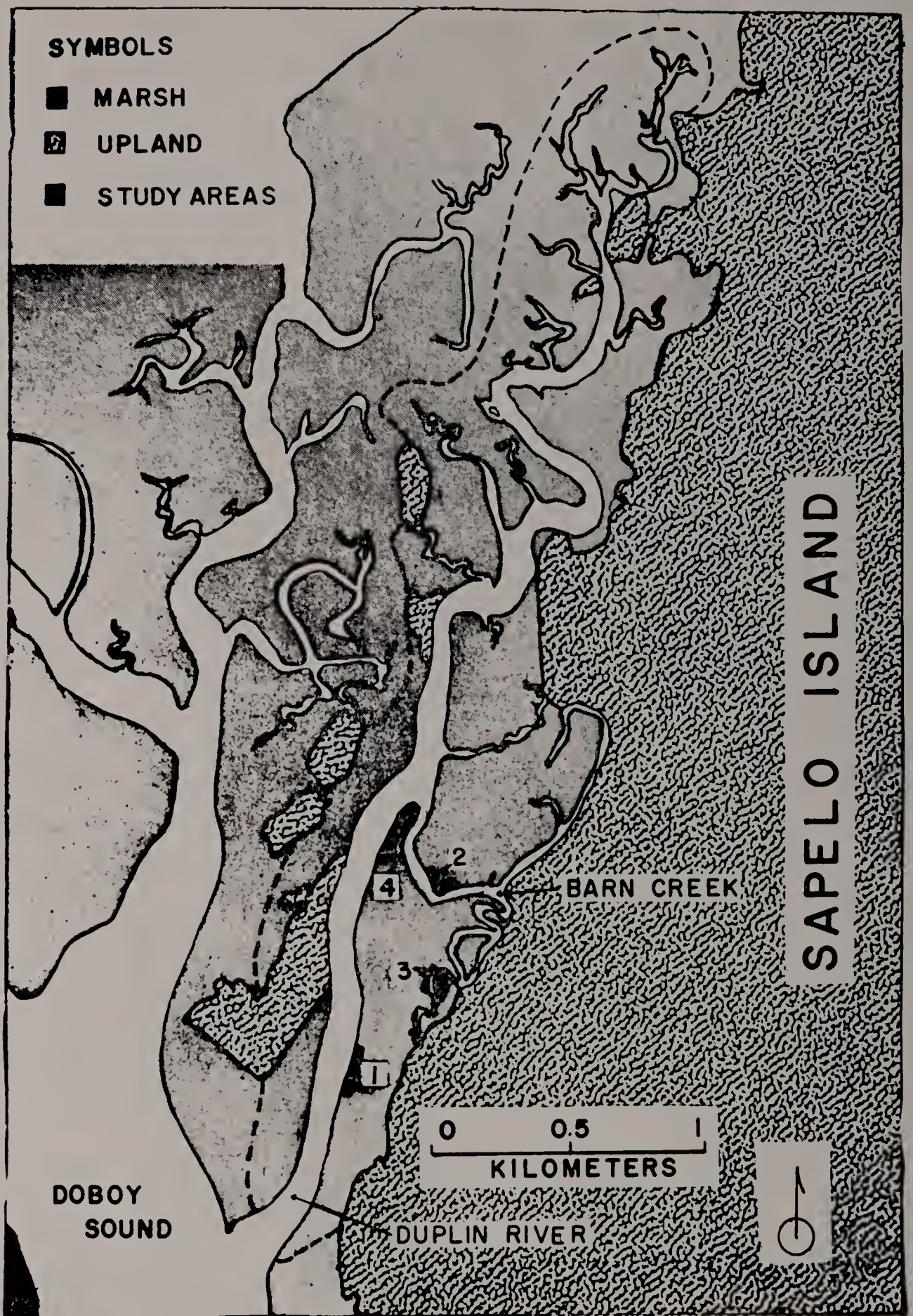


FIGURE 4. The Duplin River watershed and surrounding region at Sapelo Island. The marsh area of the watershed is outlined by the dashed line. Intensive study areas are indicated by numerals.



FIGURE 5. Wren habitat in streamside marsh along Barn Creek at low tide



FIGURE 6. Wren habitat along the Duplin River at low tide

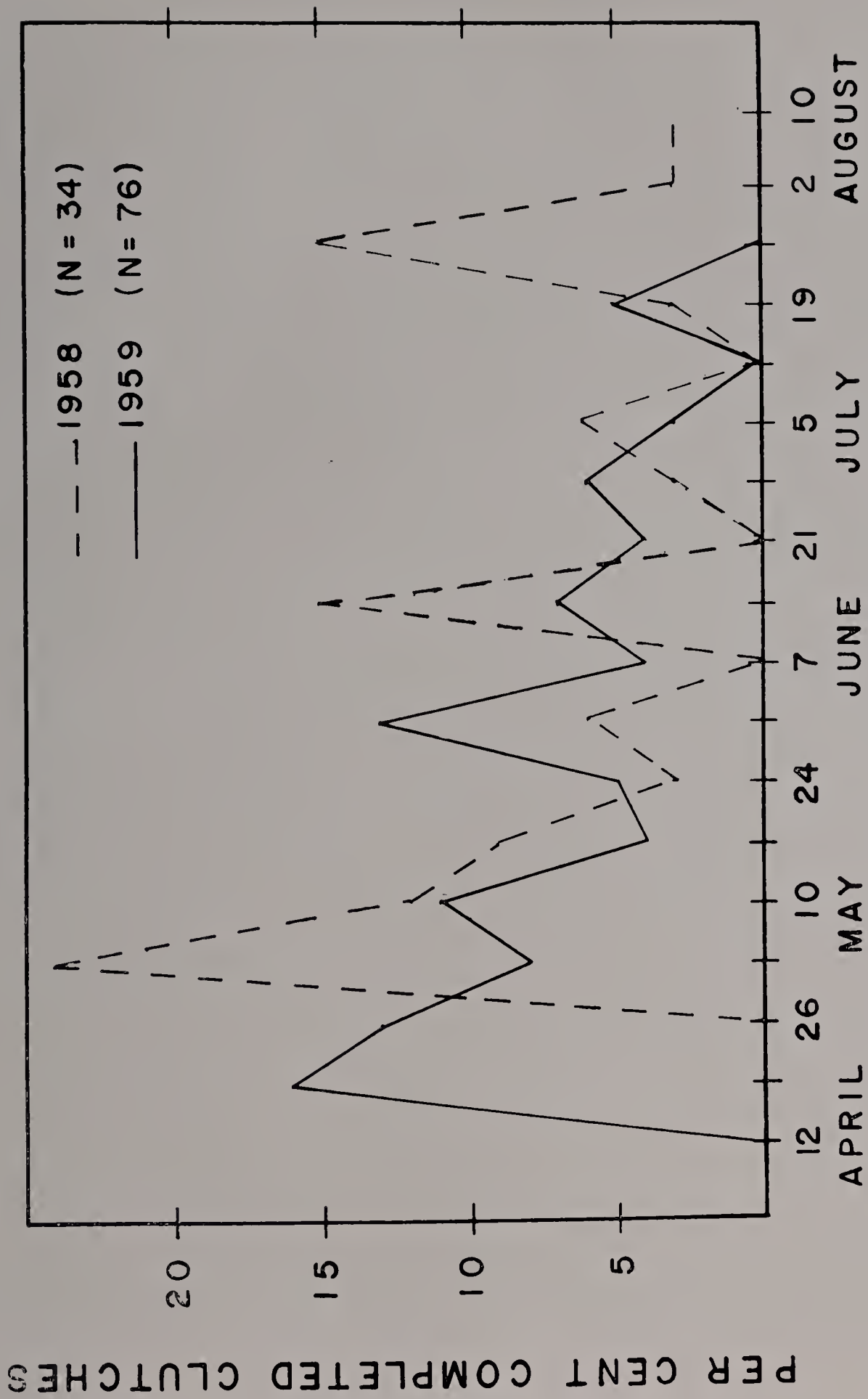


FIGURE 7. Seasonal incidence of nesting in 1958 and 1959



FIGURE 8. Nest of *T. p. griseus* in the salt marsh



FIGURE 9. Hand-reared fledgling wren on a dried marsh wren nest

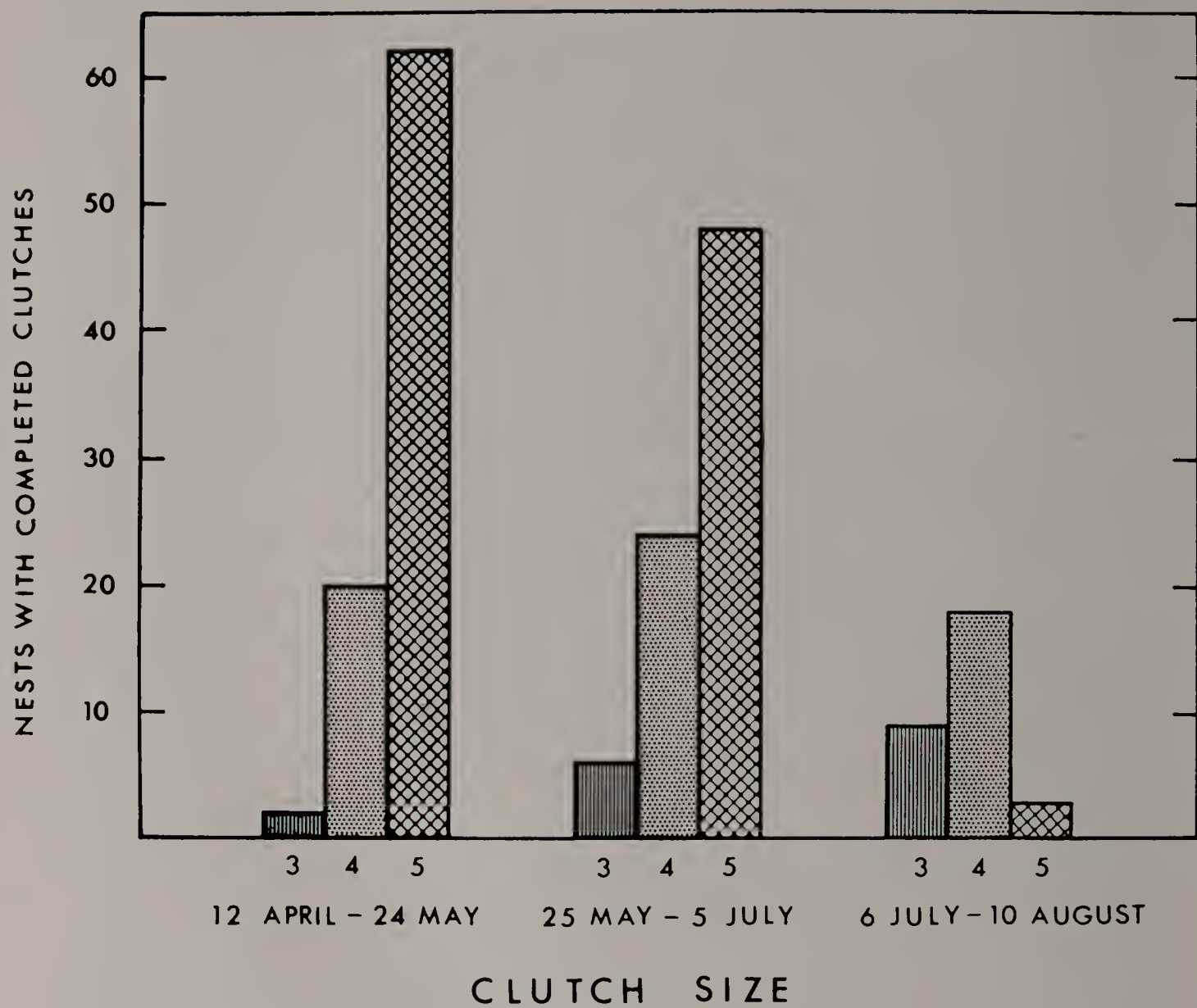
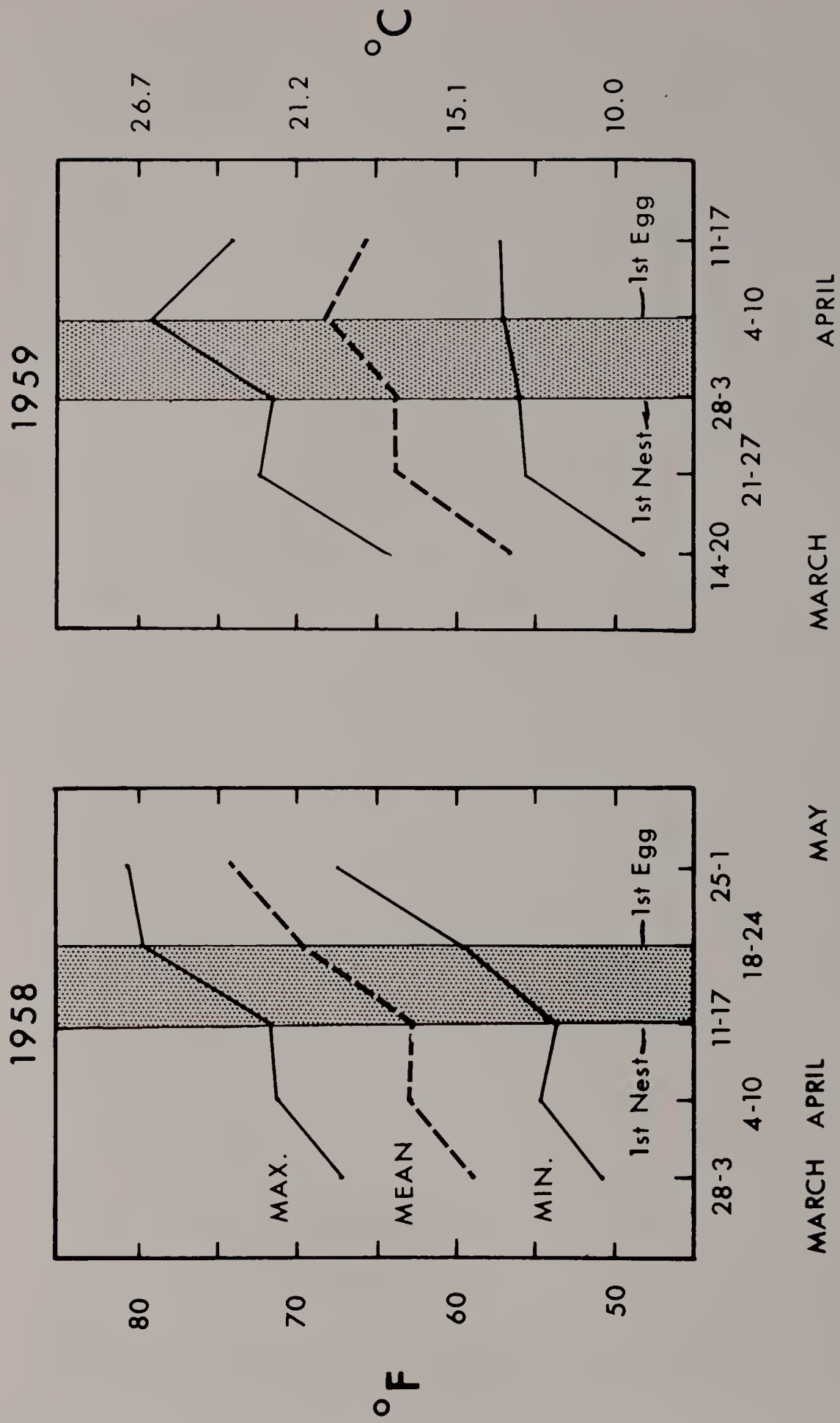


FIGURE 10. Frequency of clutch size in *T. p. griseus*

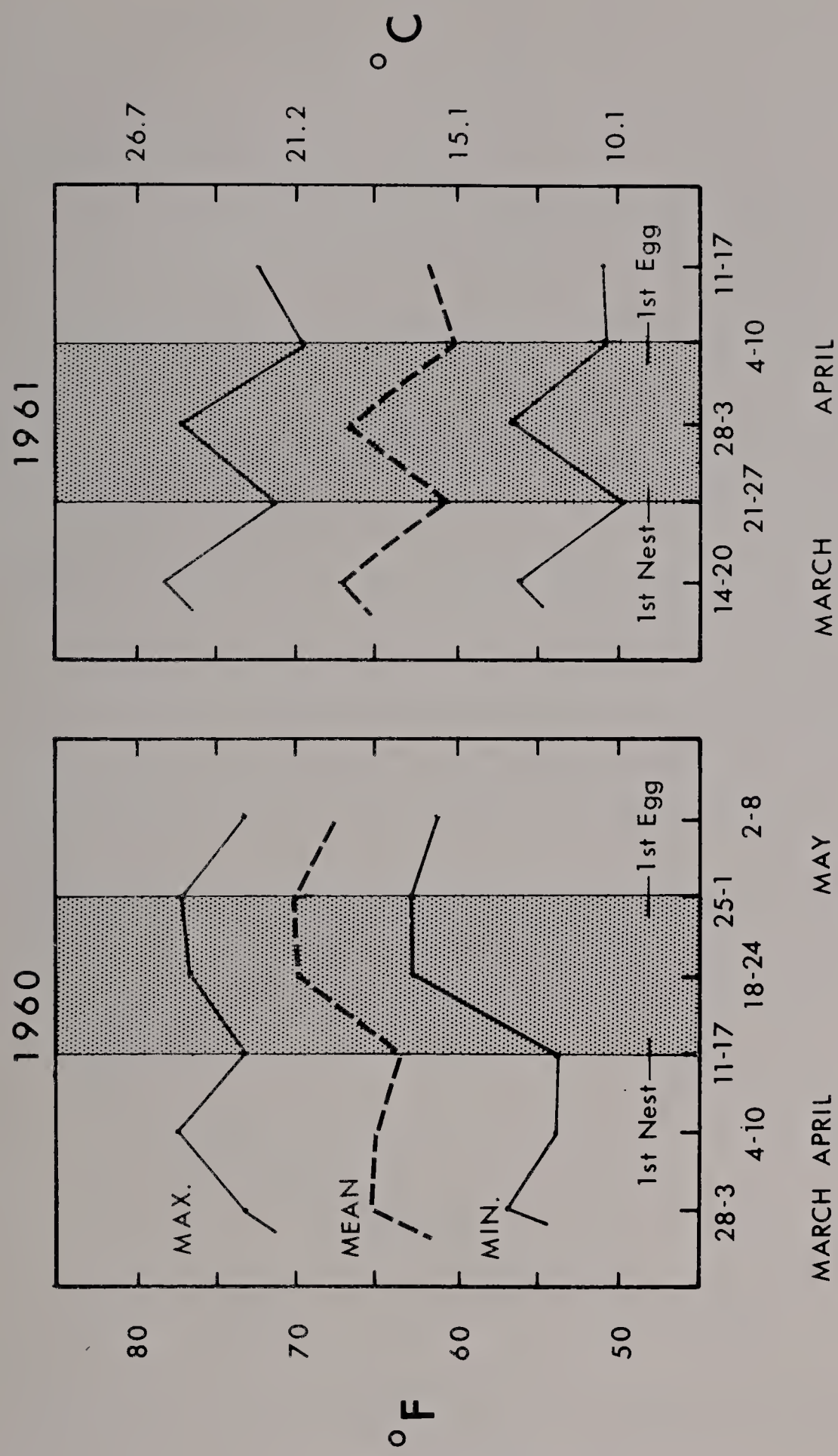


FIGURE 11. Hand-reared fledgling Long-billed Marsh Wren



INITIATION OF BREEDING

FIGURE 12. Relation of start of nesting to weekly mean temperature in 1958 and 1959



INITIATION OF BREEDING

FIGURE 13. Relation of start of nesting to weekly mean temperature in 1960 and 1961

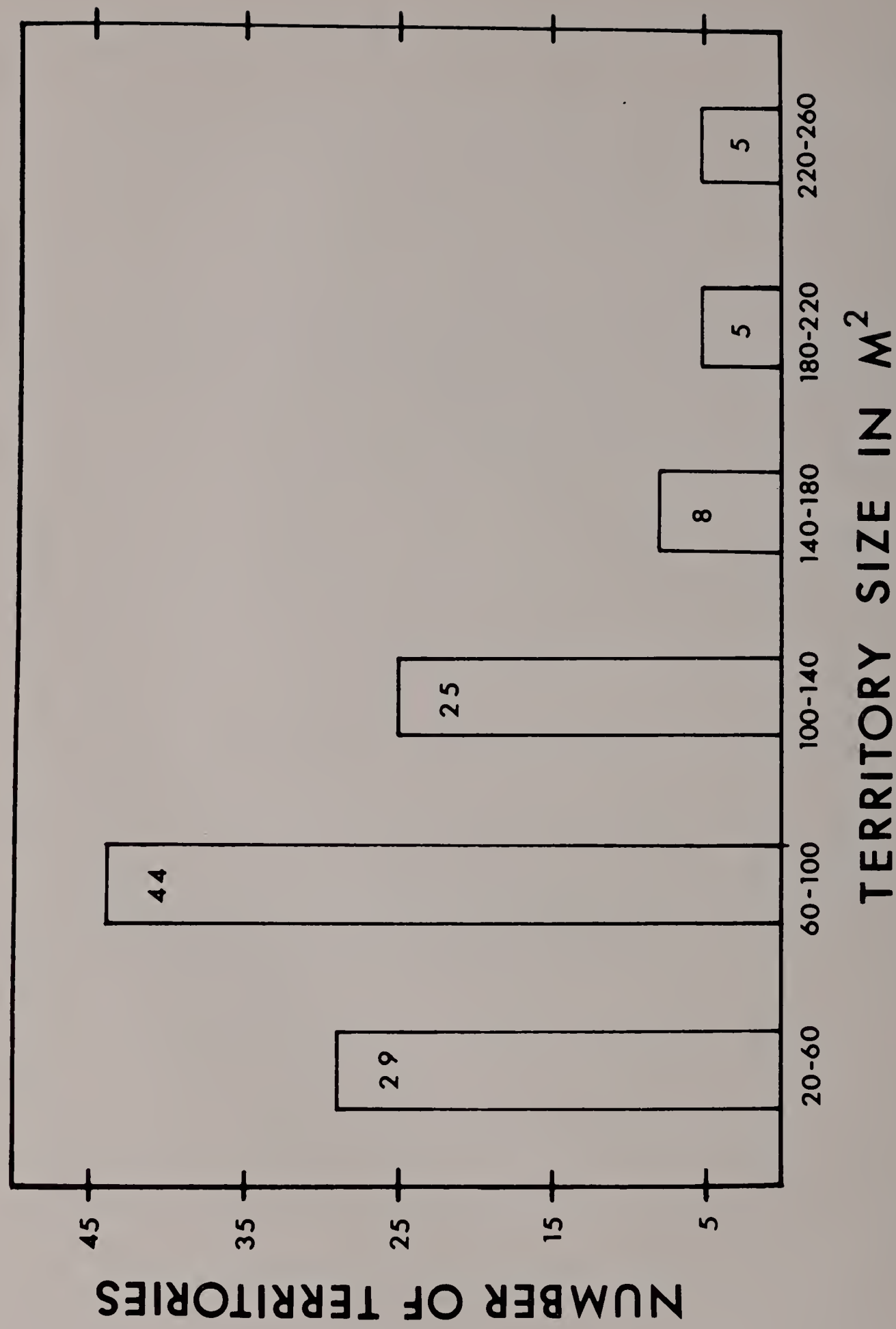
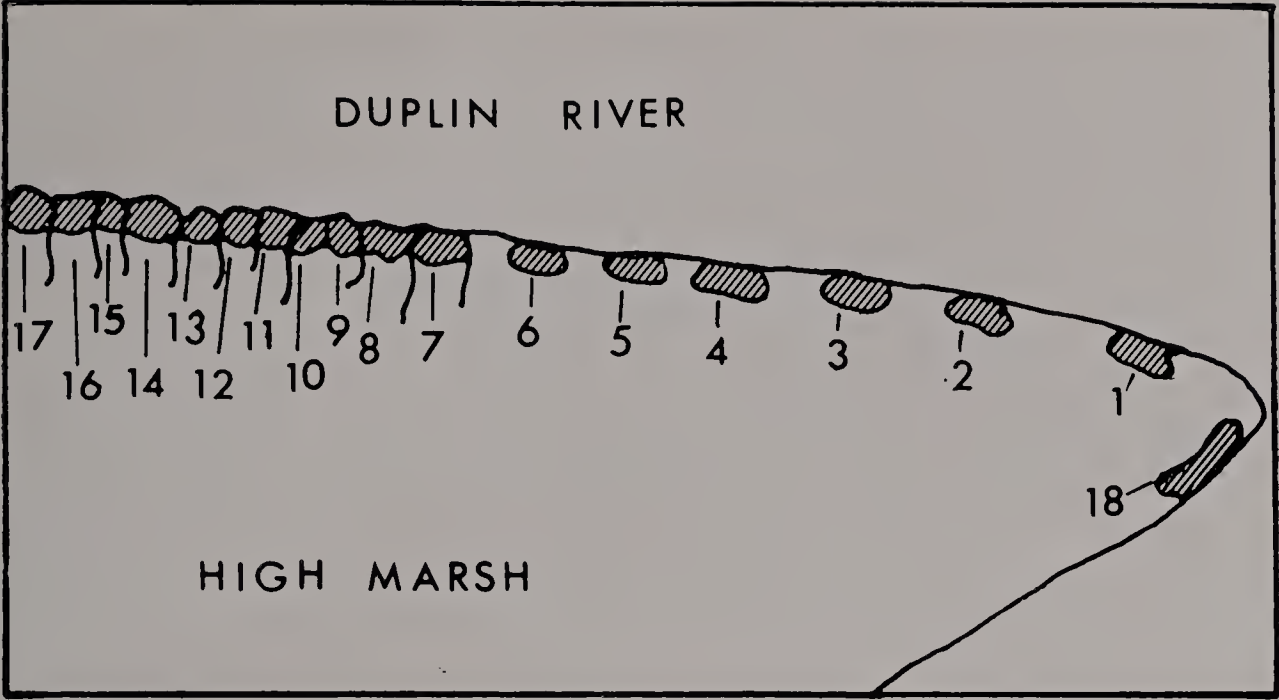


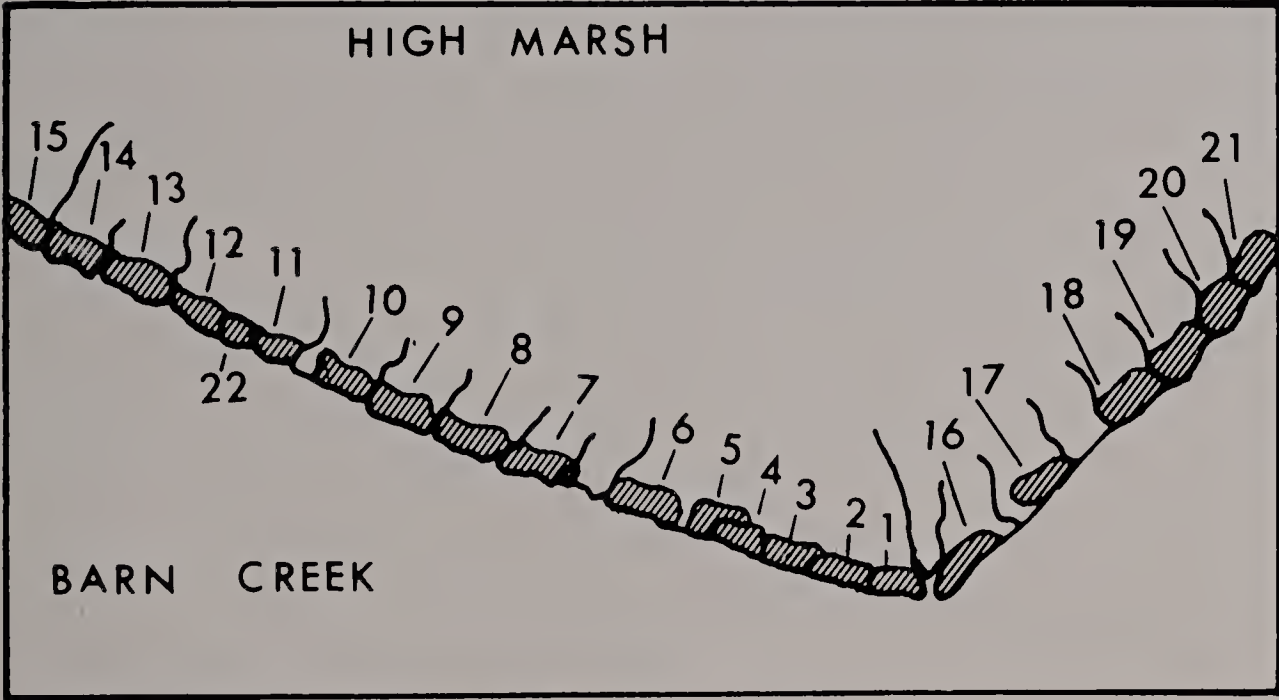
FIGURE 14. Frequency distribution of different sized territories during the 1958-1961 breeding seasons

AREA 4



0.74 KILOMETER

0.40 KILOMETER



AREA 2

FIGURE 15. Linear arrangement of territories in the study areas during 1959



FIGURE 16. Raccoon ramp built in wren habitat during period of high spring tides



FIGURE 17. Area of wren habitat in streamside marsh along Barn Creek flattened by a porpoise (Atlantic Bottlenose Dolphin) or an alligator during high tide in late June, 1959. (This photo is a view at low tide.)

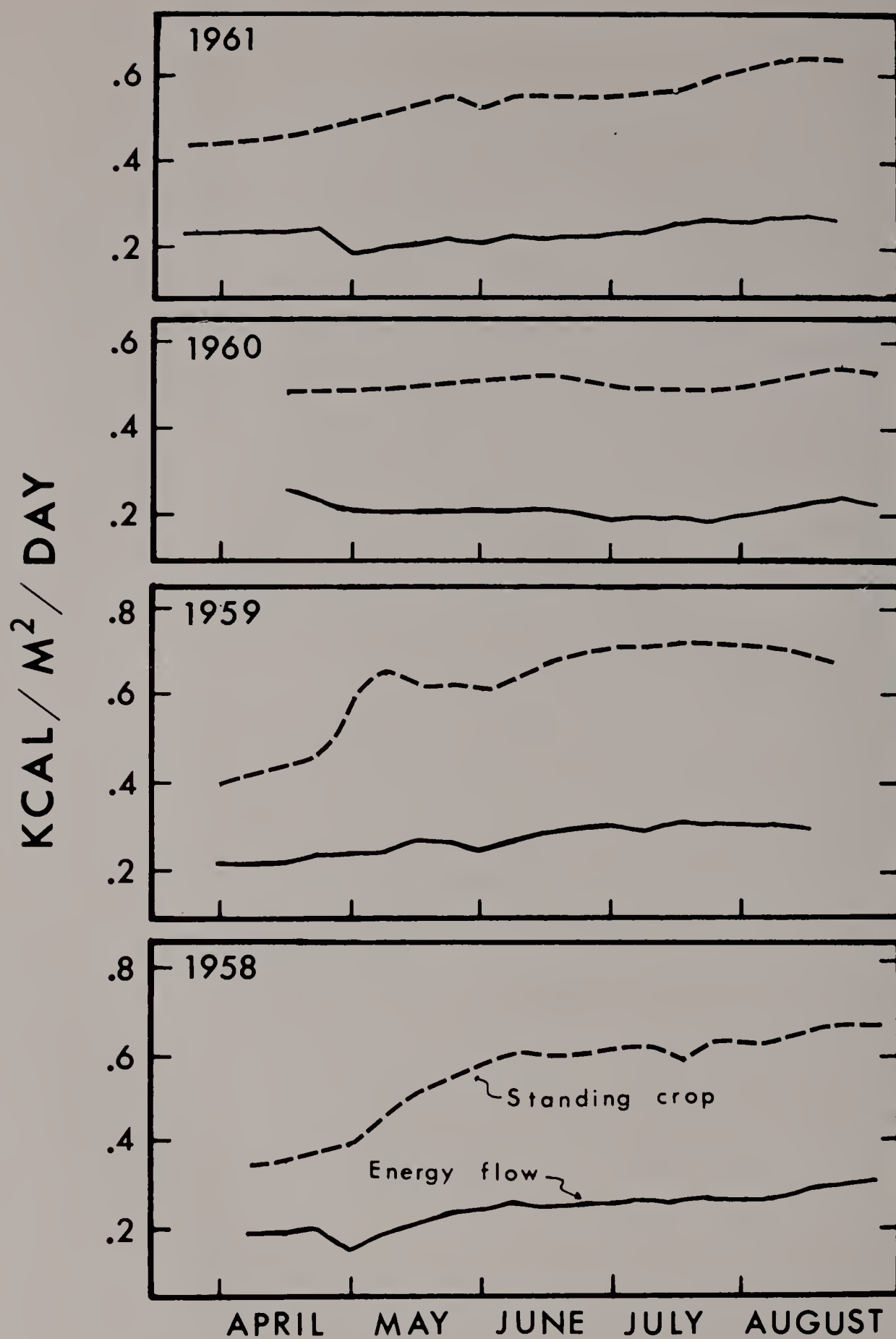


FIGURE 18. Standing crop and energy flow (assimilation) of salt marsh wrens in Kcal/m² of occupied habitat x day based on weekly census data during the breeding seasons, 1958-1961

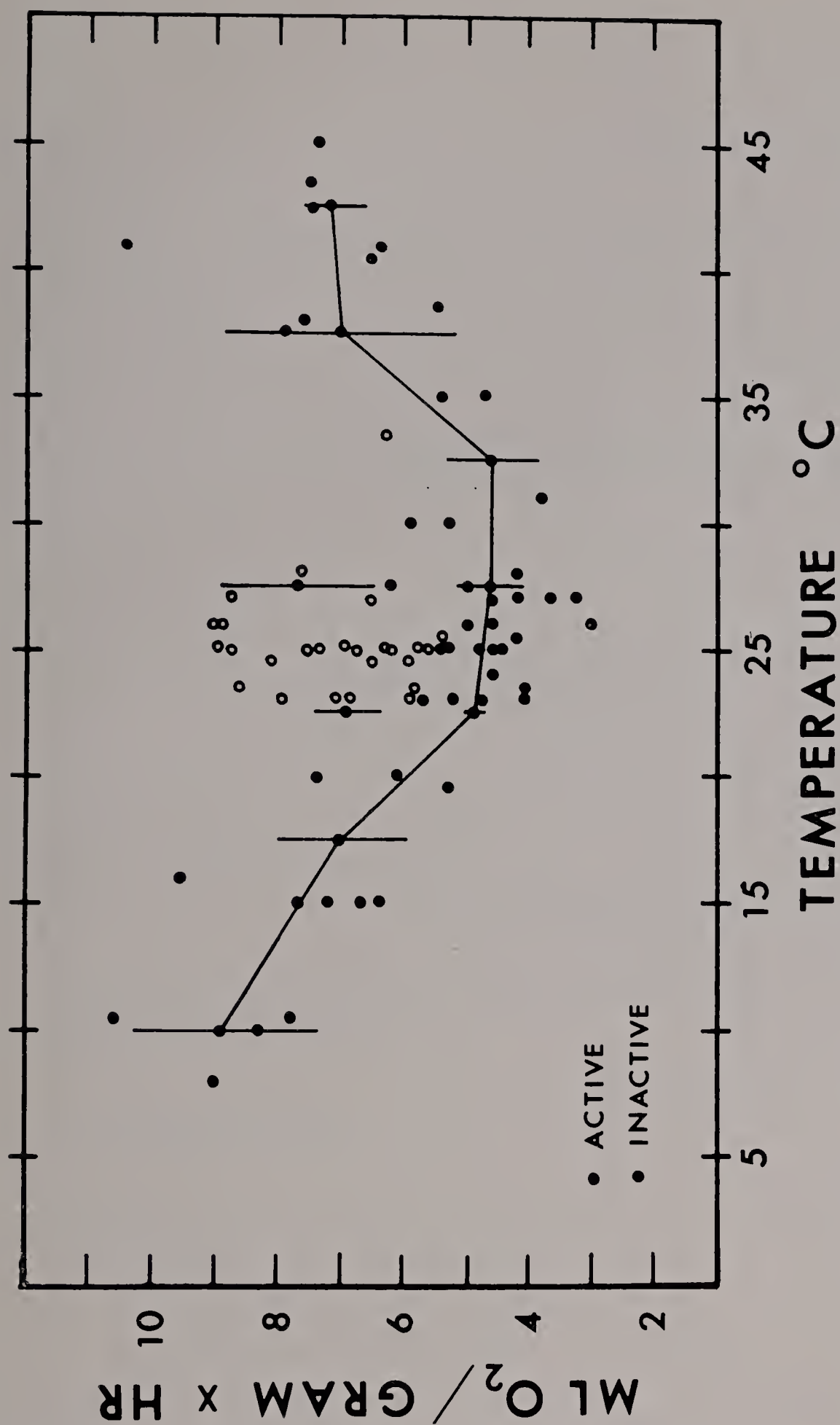
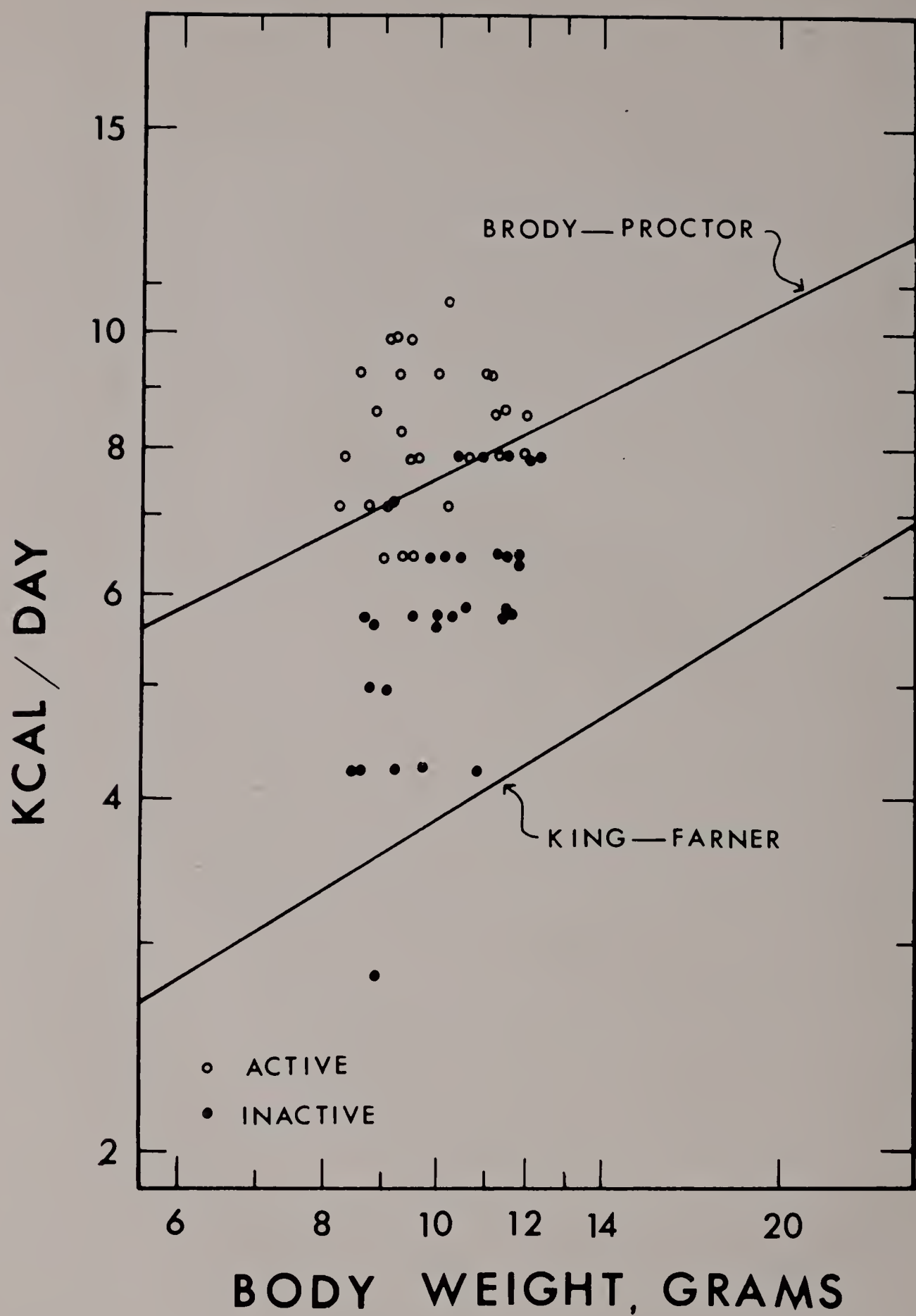


FIGURE 19. Relation of oxygen consumption in ml/gm x hr of marsh wrens to ambient temperature. Means ($\pm$ 2 standard errors) of the near-basal values for each 5° C interval (10° interval from 5-15° C) are indicated by the line connecting them. Means ($\pm$ 2 S.E.) of the metabolic rates of active wrens between 20-30° C appear above the line. (Solid circles = near-basal rates; open circles = active wrens.)



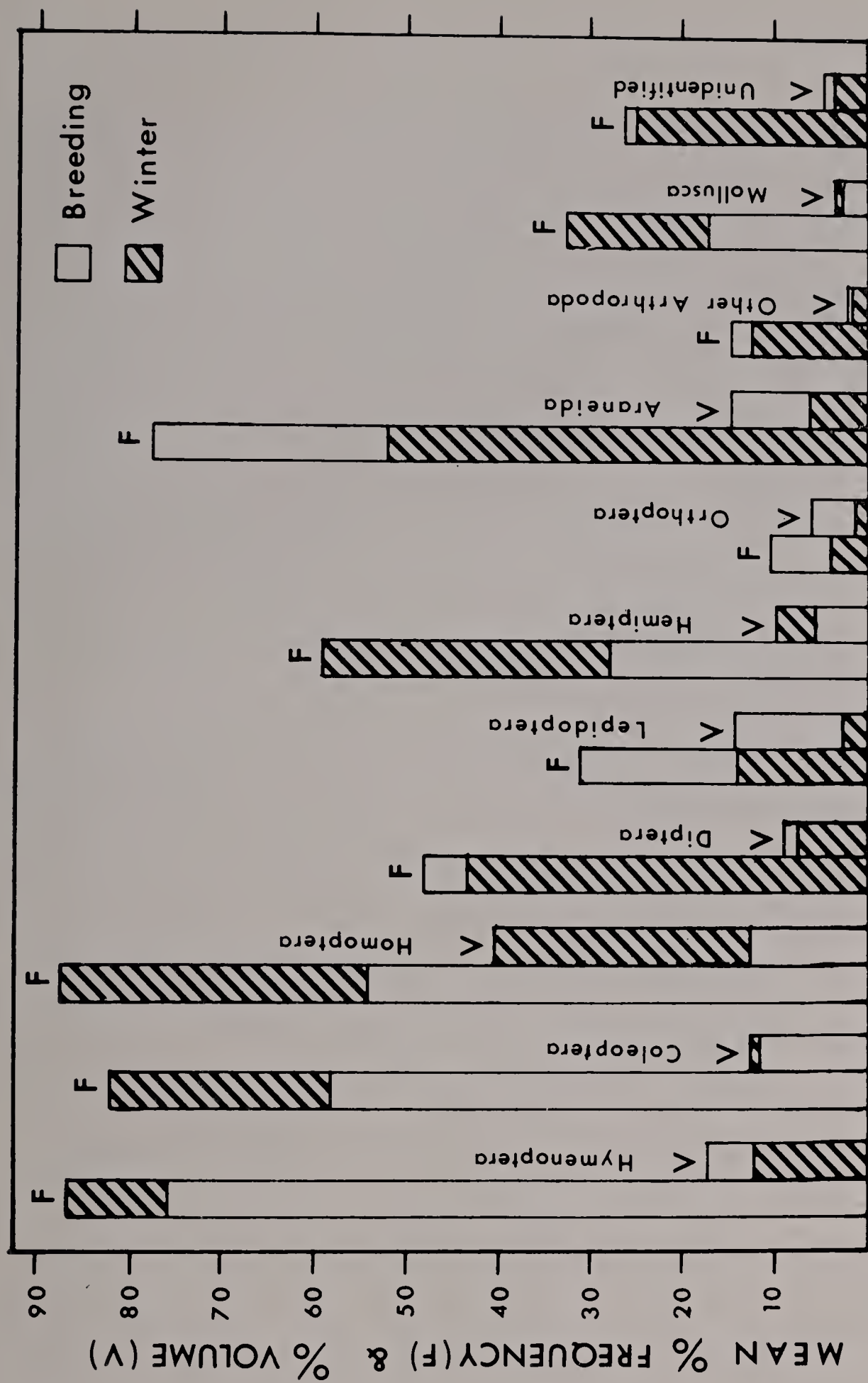


FIGURE 21. Mean percent frequency of occurrence and percent total volume of food items in 113 wren stomachs during the breeding season (April through August) and 82 stomachs during the winter season (September through March)

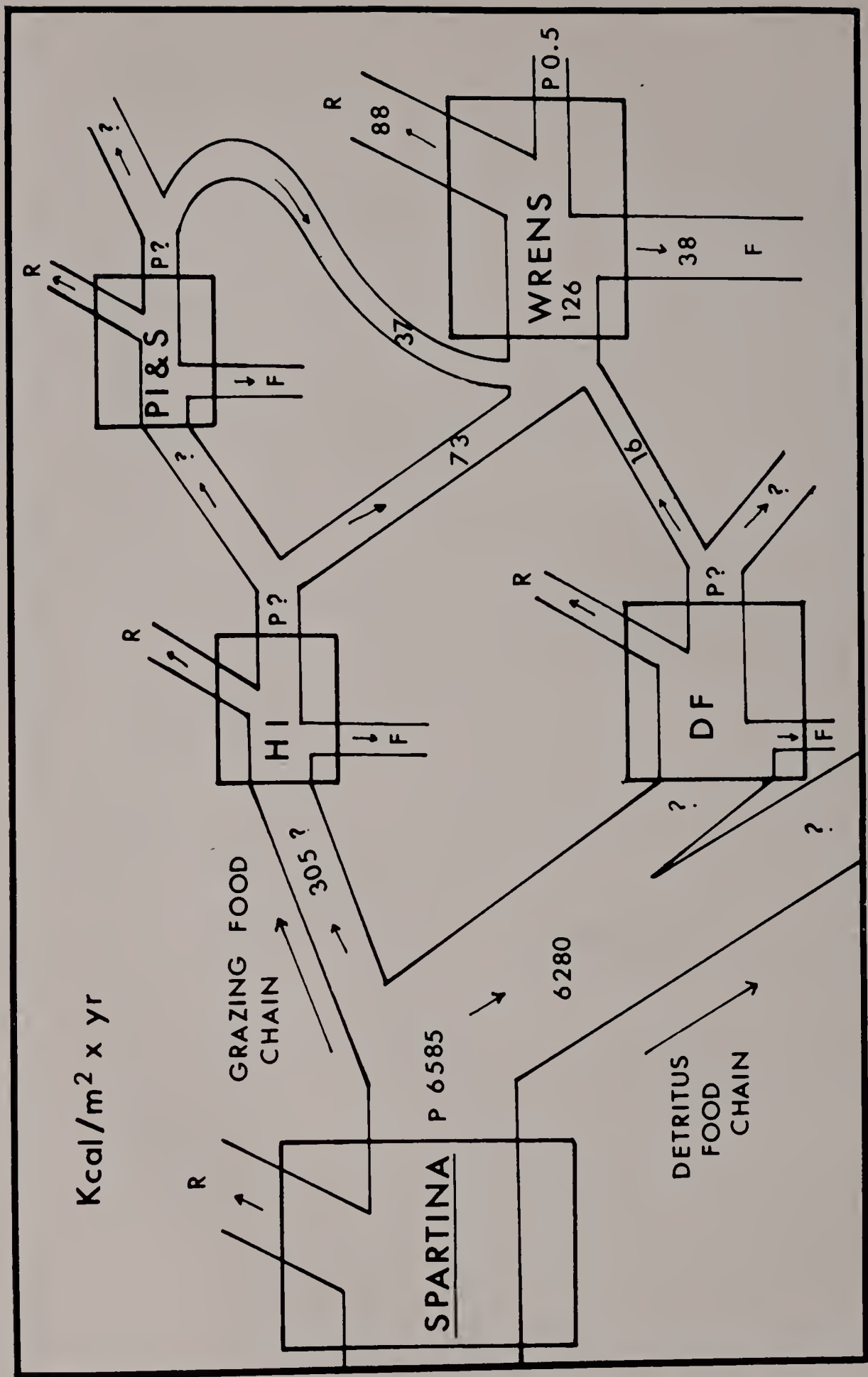
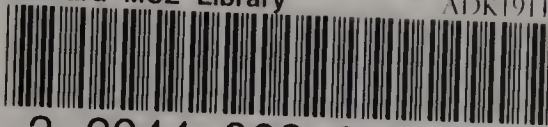


FIGURE 22. Energy flow diagram showing relationship of the wren population to the energy flow of the salt marsh. Sizes of the boxes and pipes are not proportional to size of standing crops or energy flows (HI = herbivorous insects, PI&S = predatory insects and spiders, DF = detritus feeders, R = respiration, and F = feces).

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